University of Alberta

Woodland Caribou Habitat Selection During Winter and Along Migratory Routes in West-Central Alberta

by

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Abstract

Woodland caribou (*Rangifer tarandus caribou*) are a threatened species throughout Canada. Special management is required to ensure suitable habitat is maintained. I assessed winter and spring habitat selection patterns for caribou inhabiting the Narraway range in west-central Alberta at multiple spatial scales using resource selection functions (RSFs). In winter, caribou selected habitat patches with high area to perimeter ratios and low terrain ruggedness, and forest stands with a larger component of black spruce (*Picea mariana*) and greater abundance of *Cladina mitis* (terrestrial lichen). During the spring migratory period, caribou selected travel routes through less rugged areas that were closer to water, and rested/foraged in older forests with a greater component of pine, further from water. Arboreal lichen was more abundant at resting/foraging sites than traveling sites, suggesting importance as a food resource during migration. These RSF models are important tools that can be used in land use and conservation planning.

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Chapter 1. Introduction

Woodland caribou (*Rangifer tarandus caribou*) are listed as threatened federally by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and provincially, under the Alberta Wildlife Act. As such, special management considerations must be made to ensure their habitat requirements are met, particularly since much of their current range is strongly influenced by habitat alteration from resource extraction industries. Habitat alteration and loss, climate change, and predation, have all been recognized as threats to population persistence, although predation is often considered to be a proximate contributor to caribou declines (Thomas & Gray 2002).

Woodland caribou distribution is circumpolar, and caribou display a great deal of variation in habitat use and behaviour patterns. Because of this variation, the species has been classified into ecotypes, differentiated primarily on the basis of habitat use (Edmonds 1991). There are two ecotypes of woodland caribou in Alberta: boreal and mountain. Boreal populations inhabit peatland complexes which are interspersed with upland pine forests (Edmonds 1991; Dzus 2001). Caribou of this ecotype can have distinct seasonal ranges, however ranges often overlap, and they are considered non-migratory. Mountain caribou exhibit seasonal migratory movements, spending the summer in alpine areas (Edmonds & Smith 1991), and returning to lower elevation mixed conifer forests when snow accumulates in the mountains. Regardless of the habitats used, both ecotypes depend on landscapes that support terrestrial lichen, the primary winter forage of caribou (Thomas et al. 1996; Dzus 2001). Populations of both ecotypes have

declined in past decades (Edmonds 1988; McLoughlin et al. 2003), coinciding with expansions in resource extraction industries. My research focuses on the mountain ecotype of woodland caribou, specifically those inhabiting the Narraway range, located in west-central Alberta and east-central British Columbia.

In west-central Alberta, forest harvest rights on caribou winter ranges have been allocated to industry, and are currently managed under agreements with the provincial government. The ranges are also facing cumulative pressures from the energy sector. Identification of the specific habitat requirements of caribou is therefore critical to the successful integration of caribou conservation strategies and sustainable land use practices, providing fundamental knowledge for the long-term persistence of this species.

Habitat selection models have become increasingly popular as a method of quantifying habitat requirements of species by taking into account what is used by an animal in relation to what is available to it (Manly et al. 2002). They are attractive because they can provide quantitative, spatially explicit predictive models for animal occurrence (Mladenoff et al. 1995; Manly et al. 2002). These models can inform management strategies aimed at reducing the impact of land use activities on species of concern. However, predictions generated by these models are typically restricted temporally and spatially to the landscape in which models were developed (Manly et al. 2002) and are most appropriately used as a tool within an adaptive management framework (Walters 1986). Data and logistical limitations have, until recently, prevented many models from being

validated, and in many cases, models have been applied to areas outside that which they were developed without any assessment of model prediction in the novel area. Given the tenuous state of caribou populations, it is critical that all models depicting habitat use be validated prior to implementing land-use plans based on their findings. The scale at which selection is investigated, how availability is defined, and the analytical procedures used must all be considered when interpreting these models, because all have the potential to influence the outcome of habitat selection studies (Garshelis 2000; Manly et al. 2002).

The Narraway caribou range provided a unique opportunity to study habitat selection without the confounding effects of ongoing industrial activity, as the core of the range existed in a relatively pristine state at the time this study was conducted. Although industrial development has been slow to come to the Narraway, it is now proceeding in earnest. Habitat selection models developed for this landscape could greatly facilitate the planning of these developments, such that their effect on caribou is minimized. Currently, alpine areas where caribou spend much of the summer are precluded from development, while the Narraway winter range and movement corridors between summer and winter ranges are affected by encroaching development. Consequently, I focused on habitat selection during the winter and the migratory period.

Winter ranges are thought to be the most limiting for mountain caribou and have been the primary focus of conservation efforts. While a number of earlier studies have quantified winter habitat use patterns of mountain caribou in west-central Alberta (Stepaniuk 1998; Smith et al. 2000; Oberg 2001; Szkorupa

2002), none have integrated available habitat data with other topographic and anthropogenic data sources to provide a more comprehensive assessment of habitat selection. The aforementioned studies evaluated habitat selection on ranges that had already experienced a substantial amount of industrial development; I provide an assessment of habitat selection on a range minimally affected by development, and therefore, a yardstick against which to measure the effect of future development on the Narraway caribou range. Finally, and perhaps most importantly, I was able to validate my models, giving land managers some indication of their accuracy in predicting caribou occurrence, both within the Narraway range and on an adjacent range.

Attributes of mountain caribou migratory pathways have received considerably less attention than those of winter ranges. Mountain caribou display high fidelity to both their summer and winter ranges (Schaefer et al. 2000), and if the preservation of functional caribou ranges is to be achieved concurrently with industrial development, maintaining habitat connectivity should be a priority. There are three mountain caribou ranges in west-central Alberta. Most caribou in the A La Peche range no longer migrate to their traditional wintering areas, remaining year around in the mountains (Brown & Hobson 1998), and portions of a traditional migratory route of the Redrock-Prairie Creek herd have been altered in recent years, with unknown consequences. By assessing habitat selection of caribou along migration routes linking seasonal ranges in the Narraway, connectivity between seasonal ranges can be accounted for in land-use plans, ensuring conservation efforts on the winter range are not compromised.

1. Thesis Overview

My overall objective in this thesis was to develop empirically based habitat selection models that could accurately predict the occurrence of caribou on the landscape during the winter and the spring migratory periods. I developed these models at two spatial scales, reflecting selection of coarse habitat attributes within seasonal ranges and at a finer scale, selection of potential forage species. The first scale corresponds to the level at which management takes place, and the second provides insight into the mechanisms driving selection at higher scales.

In Chapter 2, I investigate caribou habitat selection within the winter home range, and the fine-scale vegetation characteristics associated with these sites, emphasising caribou forage species. This was accomplished using a combination of global positioning system and geographic information system technologies together with field sampling.

In Chapter 3, I explore habitat selection during the spring migratory period, incorporating caribou behaviour into the modelling process on the basis of movement rates. Again, this analysis was carried out at multiple scales.

Finally, Chapter 4 highlights my major findings, provides management recommendations and applications, and offers direction for future research.

2. Literature Cited

Brown, W. K. and D. P. Hobson. 1998. Caribou in West Central Alberta - Information Review and Synthesis. Prepared for West-Central Alberta Caribou Standing Committee. Terrestrial & Aquatic Environmental Managers ltd. Calgary, AB. 1-104 pp.

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, Alberta. 47pp.

Edmonds, E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. Canadian Journal of Zoology **66** :817-826.

Edmonds, E. J. 1991. Status of woodland caribou in western North America. Rangifer, Special Issue **7**:91-107.

Edmonds, E. J. and K. G. Smith. 1991. Mountain caribou calf production and survival, and calving and summer habitat use in west-central Alberta. Alberta Environment, Fish and Wildlife Division, Wildlife Research Series No. 4. Edmonton, Alberta. 1-16 pp.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. *In*: Research techniques in animal ecology: consequences and controversies. L. Boitani and T. K. Fuller, *eds*. Columbia University Press, New York, NY. USA. Pp 111-164.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.

McLoughlin, P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management **67**:755-761.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great-Lakes region. Conservation Biology **9**:279-294.

Oberg, P. R. 2001. Responses of mountain caribou to linear features in a west-central Alberta landscape. MSc Thesis, University of Alberta, Edmonton Alberta, Canada.

Schaefer, J. A., C. M. Bergman, and S. N. Luttich. 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology **15**:731-739.

Smith, K. G., E. J. Ficht, D. Hobson, T. C. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear- cut logging in west-central Alberta. Canadian Journal of Zoology **78**:1433-1440.

Stepaniuk, D. W. 1997. Planning for woodland caribou winter habitat needs in west-central Alberta. MSc Thesis, University of Alberta, Edmonton, Alberta, Canada.

Szkorupa, T. D. 2002. Multi-scale habitat selection by mountain caribou in west central Alberta. MSc Thesis, University of Alberta, Edmonton Alberta, Canada.

Thomas, D. C., E. J. Edmonds, and W. K. Brown. 1996. The diet of woodland caribou populations in west-central Alberta. Rangifer, Special Issue **9**:337-342.

Thomas, D. C. and D. R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada, in COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 1-98 pp.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillian Publishing Company. New York, New York, USA.

Chapter 2. Multi-Scale Winter Habitat Selection by Mountain Caribou

1. Introduction

Woodland caribou (*Rangifer tarandus caribou*) populations are declining throughout their range. The species has been listed federally as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and is classified as threatened in Alberta under the Provincial Wildlife Act. While numerous factors have been associated with the historic decline of woodland caribou, habitat alteration due to resource development has caused the most concern (Bradshaw et al. 1997; James & Stuart-Smith 2000; Smith et al. 2000; McLoughlin et al. 2003). Habitat requirements of woodland caribou are believed to be incompatible with the forest conversion and fragmentation that accompany development. Conflicts between caribou conservation and industry are three fold. Woodland caribou require old growth forests that contain lichens, their primary winter food source (Bjorge 1984; Stevenson 1990; Thomas et al. 1996). These forests are also valuable to the forest industry (Terry et al. 2000). Caribou also require large patches of forest in which to distribute, both separating themselves from each other and from other ungulate species (Bergerud & Page 1987; Bergerud 1990; James et al. 2004). This makes caribou vulnerable to forest fragmentation. Finally, the proliferation of linear features associated with development, such as roads, seismic lines, and pipelines may have negative implications for caribou due to increased disturbance, human caused mortality, and predation by wolves (*Canis lupus*; James & Stuart-Smith 2000).

All caribou ranges in west-central Alberta are allocated under forest management agreements and a high proportion of each range has been leased for

petroleum exploration and development. Oil and gas activities within caribou ranges operate under the spirit of a provincial government information letter (IL 91-17). This letter states that "industrial activity could occur on caribou range provided that the integrity and supply of habitat is maintained to permit its use by caribou" (Alberta Energy 1996). In west-central Alberta, old growth forest typical of that which supports caribou is still relatively abundant, but the demand on the land base continues to grow.

Current industrial operations in west-central Alberta are concentrated in low elevation areas. As such, the winter ranges of caribou populations are most affected. Caribou display high fidelity to their winter range (Schaefer et al. 2000), and the availability of suitable habitat adjacent to current ranges has not been demonstrated. If suitable alternate areas are not available, the potential is limited for range shifts in response to habitat alteration (Schaefer & Pruitt 1991; Nellemann & Cameron 1998). Therefore, maintaining high quality, functional habitat within current winter ranges is the primary focus of conservation plans. If industrial operators are expected to consider caribou habitat requirements in their management plans, then a better understanding of those requirements is needed.

Resource selection functions (RSFs; Manly et al. 2002) have become increasingly popular in recent wildlife literature as a framework for examining habitat use (e.g., Compton et al. 2002; Nielsen et al. 2004; Johnson et al. 2004b). They are attractive because they can provide quantitative, spatially explicit predictive models for animal occurrence (Mladenoff et al. 1995; Manly et al. 2002). However these predictions are restricted temporally and spatially to the

landscape in which models are developed (Manly et al. 2002). Despite this clear limitation, data deficiencies and logistical issues regularly preclude model validation and models are often applied to regions beyond their inference without an assessment of the accuracy of prediction. Failure to incorporate model validation and tests for generality prior to the use of models can lead to erroneous management decisions.

Some reviews have highlighted the need for occurrence models to incorporate the underlying mechanisms that drive the selection process (van Horne 1983; Morrison 2001). Examples of these underlying mechanisms include availability of forage resources, availability of suitable breeding habitat, and competitive factors (Morrison 2001). These factors heavily influence habitat quality, ultimately determining occupancy, survival and recruitment (Morrison 2001). Understanding these mechanisms and including them in occurrence models may improve model performance across time and space. With respect to caribou, the occurrence of food resources is thought to be critical in determining caribou distribution. Caribou are particularly dependent on terrestrial lichens during winter (Bjorge 1984; Thomas et al. 1996; Rettie et al. 1997), when they make up approximately 72% of the diet (Thomas et al. 1996). This being the case, the winter distribution of caribou should be associated with that of terrestrial lichens and the inclusion of lichen occurrence in caribou models should improve model fit. If important caribou forage species can be identified and their occurrence mapped, they can be accounted for during the planning process and impacts to these areas minimized.

To identify attributes influencing the distribution of caribou while on the winter range, I developed coarse and fine scale RSFs, corresponding to Johnson's 3rd and 4th

orders of selection respectively (Johnson 1980), for caribou using the Narraway Range in west-central Alberta. Coarse-scale selection refers to the use of habitat components within a home range while fine-scale reflects selection of forage items (Johnson 1980). The specific objectives of this project were to 1) identify fine-scale habitat attributes that caribou select while on the winter range; 2) understand and predict forage species occurrence across the Narraway winter range; 3) identify coarse-scale habitat attributes associated with winter range habitat use and; 4) test the robustness of resultant models through validation and generalization on a second caribou range in west-central Alberta, occupied by the Redrock-Prairie Creek herd. In the context of this study, habitat is defined as the set of specific environmental conditions associated with animal use and habitat use is defined as the extent to which different environmental states are used (Garshelis 2000). Habitat selection depends on habitat availability and accessibility (Manly et al. 2002) and refers to the use of environmental states proportionately more then they are available (Garshelis 2000; Manly et al. 2002).

2. Study Area

I focused on woodland caribou using the Narraway winter range, approximately 1,600 km^2 in size, and located between 54° 20′ and 54° 40′ N, spanning the British Columbia-Alberta provincial boundary approximately 130 km southwest of Grande Prairie, Alberta (Figure 2.1). From a regional perspective, this range is unique in that, at the time this research was conducted it existed in a relatively pristine state, with only minor industrial development. Most animals winter

on a large plateau between the Narraway River and Huguenot Creek. Much of this area is poorly drained and dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Within this central muskeg area are patches of upland forest dominated by lodgepole pine (*Pinus contorta*) and black spruce. Elevation ranges between 733 m and 2018 m above sea level. The caribou population on this range has been estimated at 100 individuals, although confidence in this estimate is low and the population trend is unknown (Thomas & Gray 2002).

The Redrock-Prairie Creek (RPC) winter caribou range is located southeast of the Narraway winter range and is approximately 2,200 km^2 in size. The core of the range is along the eastern edge of the Rocky Mountains, bisected by the Kakwa River. It is located primarily in the upper foothills ecoregion (Beckingham & Archibald 1996) and consists of many upland ridges interspersed with lowland drainages. The caribou population on the RPC range has been estimated at 312 individuals with a moderate amount of confidence and the population trend is thought to be stable to decreasing (Thomas & Gray 2002).

At the time of this study, the RPC had a higher level of industrial development, particularly along its eastern edge, compared to that on the Narraway range. Forest harvesting on the RPC range began in 1976 and there has been extensive oil and gas exploration and development activity. In addition to caribou, both ranges also support moose (*Alces alces)*, white- tailed deer (*Odocoileus virginianus*), and small numbers of elk (*Cervus elaphus*). Large carnivores that inhabit the ranges include coyote (*Canis latrans*), wolves (*Canis*

lupus), cougars (*Felis concolor*), grizzly (*Ursus arctos*) and black (*Ursus americanus*) bears.

3. Methods

3.1. Caribou Location Data

Eighteen adult female caribou using the Narraway range were captured using helicopter-based net gunning techniques from October 2000 – October 2003. All capture and handling methods were approved by the University of Alberta, Faculty of Agriculture, Forestry and Home Economics Animal Policy and Welfare Committee (Protocol 2003-29D) and adhered to guidelines outlined by the Canadian Council on Animal Care. Caribou were outfitted with differentially correctable global positioning system (GPS) collars (Lotek GPS 1000 or Lotek GPS 2200, Lotek Engineering, Inc., Newmarket, Ontario, Canada.). Collars were programmed to acquire a fix on one of two schedules: a standard two-hour schedule or a variable schedule in which locations were acquired every 30 minutes, 2 hours, or 6 hours, depending on the day of the week. All locations with HDOP (horizontal dilution of precision) values greater than 12, indicating poor locational accuracy, were removed prior to analysis. The number of winter (December 1 - April 30) locations analyzed was reduced from 14, 353 to 726 to minimize autocorrelation. To maintain consistency with previous work conducted in the region (Szkorupa 2002), I chose to use daily locations acquired at 1200hrs $\pm$ 2hrs if noon locations were not available. Only locations that were spatially (> 1 km) and temporally independent of other collared caribou were included in the analysis. Data used for validation or generalization had the same restrictions applied.

3.2. Habitat Sampling

3.2.1. Fine-Scale Habitat Attributes

Fifty randomly chosen winter locations (December 2002-April 2003), representing the use sites of 6 caribou, were sampled during July and August 2003. A random site, located within a buffer equal to the average daily (Arthur et al. 1996) distance travelled by all collared caribou on the Narraway range during the winter of 2002-2003 (912 m), was paired with each of these sites. At both use and random sites I measured local vegetation characteristics. I centred a 30 X 30 m plot at each of the 100 locations. Plot dimensions incorporated GPS collar error, which has been estimated at between 5 and 30 m (D'eon et al. 2002). Used and random sites were sampled on the same day. Variables measured at each plot included canopy cover, slope, aspect and elevation. Within each plot, I randomly placed 6 quadrats. Each quadrat was 1 m^2 and measurements taken at this scale were focused on potential caribou winter forage species. I estimated percent vegetation cover for the following categories: terrestrial lichen, moss, forbs, shrubs < or > 10 cm in height, coarse woody debris, bare ground, litter, tree bole, and suspended woody debris. Terrestrial lichens were identified as *Cladina mitis, Cladina rangiferina, Cladina spp., Cetraria spp., Cladonia spp., Peltigera spp., Stereocaulon spp.,* and other lichen. Ground layer components (total lichen species, moss, forbs, shrubs < 10 cm, coarse woody debris, bare ground, litter, and tree bole) summed to100%.

In association with each of the quadrats, I estimated the arboreal lichen load below 2.5 m on the tree closest to the center of the quadrat, using broad ordinal classes (Armleder et al. 1992). These classes range from 0-5, with 0 indicating no arboreal

lichen present. A height of 2.5 m reflects what would reasonably be available as forage for caribou throughout the winter, given a maximum snow depth of about one meter in the study area (Edmonds 1988).

I averaged all measurements made at the quadrat level and assumed this value to be representative of the plot. Analysis of data from a pilot study connected with this project indicated that six quadrats would adequately represent the plot in terms of total lichen cover (D.J. Saher unpub. data).

3.2.2. Stand-Level Food Resource Plots

To incorporate the perceived importance of terrestrial lichen into higher-level selection models, I modelled the probability of food resource occurrence at the stand level. In addition to the plots sampled in association with fine-scale caribou habitat selection (n = 100), I had data from 240 plots from a pilot year (2002; total n = 340). These additional plots were sampled following the same methodologies outlined above but were located through a stratified random sampling process, based on habitat type. Forest stands were classified on the basis of leading species, stand age, and stand density; attributes thought to be associated with caribou occurrence (Thomas et al. 1996; Rettie et al. 1997; Szkorupa 2002). I restricted inference with respect to the occurrence of food resources to those habitat classes in which the combined sampling intensity was proportional to availability.

The stand level habitat attributes necessary for caribou coarse-scale model building were obtained by intersecting the plot locations with available digital forest

cover and other spatial data using Hawth's Analysis Tools Extension (Version 2) in ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, CA, USA). All digital data were projected in Nad 27, Zone 11. A grid size of 30 m was used for all environmental and forest cover data, encompassing potential errors associated with GPS collar locations (D'eon et al. 2002). These data included distance, terrain, and habitat information. Slope, aspect and distance functions were calculated in the Spatial Analyst extension in ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, CA, USA). I used a terrain ruggedness index (TRI) modified from Nellemann and Fry (1995) to account for local topographic variation. This was calculated using a 300-m circular moving window and the formula:

$$TRI = \frac{(\text{Aspect Variation} * \text{Average Slope}) / (\text{Aspect Variation} + \text{Average Slope})}{100}, \quad [1]$$

where aspect variation was the proportion of total number of aspect classes in the moving window over the maximum number of aspect classes within the available landscape (Tuner 1989).

3.2.3. Coarse-Scale Habitat Attributes

The stand level attributes associated with caribou occurrence were obtained following the same methods outlined in Section 3.2.2. Random locations were generated within a circle centered on the use location with a radius equal to the 90th percentile of the daily distance traveled by all radio-collared

caribou (Arthur et al. 1996) during the winters of 2002-2004 (2.4 km) using Hawth's Analysis Tools extension (Version 2.0) in ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, CA, USA). Twenty random points were generated for every sampled use location (King & Zeng 2001).

Digital data layers were created on a yearly basis to take into account landscape change due to forest harvesting. Analysis at this scale includes patch configuration variables, for example distance to edge and area-perimeter ratio. I defined natural edges as any naturally occurring, non-forested polygon (e.g., lakes, alpine habitat, meadows). If a polygon was classified as forest but had a stand density less than 10%, a stand age of less than 30 years, or had a deciduous component of greater than 70%, it was also classed as a natural edge. I assumed that caribou would distinguish these forest classes. The area and perimeter of land cover polygons was calculated in two different ways, both of which I felt could reflect the way a caribou might perceive its environment: first, in terms of habitat categories, defined by leading species, stand density (4 classes), and stand age (2 classes), and secondly, by broader categories defined as either forested or edge polygons. In this instance, edge includes both natural and anthropogenic edges (seismic lines, roads, well pads and cut blocks). Which definition was the better predictor of caribou occurrence on the landscape was determined through univariate logistic analysis.

3.3. Modelling Strategy

A conceptual diagram of the modelling process is illustrated in Figure 2.2. Model structure depended on the scale and response variable in question (caribou or forage resource occurrence). First, all predictor variables were examined for collinearity using Pearson correlations. Collinearity between individual parameters was assumed if correlations were > |0.7|. Within pairs of correlated variables, those that explained the most deviance from the null model when run in a univariate model were retained. Secondly, to further reduce the number of variables included in the model building process, I ran univariate regressions of the appropriate form on all remaining covariates, assessing used and available sites (Zielinski et al. 2004). Those with relatively important β values ($P < 0.25$ threshold; Hosmer and Lemeshow 2000) were retained as potentially important in distinguishing used and available sites.

Rather than developing a series of null hypotheses, I followed the multiple working hypotheses paradigm (Chamberlain 1965; Anderson et al. 2000) and developed a set of *a priori* candidate models, based on the remaining covariates. I tested all models for multicollinearity (Menard 1995) using variance inflation factors (VIF). Multicollinearity was a concern if individual parameter VIF values were > 10 or if the mean VIF score for a given model was considerably larger than 1 (Chatterjee et al. 2000). If models exhibited multicollinearity they were removed from the candidate set. The top model in each candidate set was selected using an information theoretic approach, AIC (Akaike's Information Criteria), or AIC_c when sample sizes warranted (Burnham & Anderson 2002).

This method balances model fit with model parsimony. Models were then ranked based on the difference in AIC values (ΔAIC), and Akaike weights (w_i) were used to assess the strength of evidence that any particular model was the best of those in the candidate set. I assessed the effect of the parameters in the AIC-selected model using 95% confidence intervals; coefficients whose confidence intervals did not overlap zero contribute to the model.

Previous research has indicated a non-linear relationship between canopy cover and lichen occurrence (Pharo & Vitt 2000), and between canopy cover and age and caribou occurrence (Szkorupa 2002). If the quadratic form of these variables provided a better explanation of the data (decreased AIC values) than did the base alone, the combination was used in model building.

I tested all models for nonlinearity of the logit and influential outliers (Maynard 1985) and they were adjusted if necessary. Analyses were carried out using the statistical package STATA 8.2 (Stata Corporation).

3.3.1. Fine-Scale Caribou Models

I developed resource selection functions (RSF; Manly et al. 2002) at the fine-scale using case-control logistic regression. This analytical approach accounts for the spatial and temporal variation in habitats (Pendergast et al. 1996; Compton et al. 2002) by restricting availability to that associated with each use site. Attributes associated with a use site are compared only against those of linked random sites (Cooper & Millspaugh 1999), reducing the effects of autocorrelation (Pendergast et al. 1996; Compton et al. 2002). As individual

animals were marked, and available points were constrained by the use location, the analysis followed the Design IV approach of Erickson et al. (2001).

Analysis was carried out following a 1:1 matched case design and model structure followed the form:

$$w(x) = \exp(\beta_1 x_{ij1} + \beta_2 x_{ij2} + \ldots \beta_K x_{ijK}), \qquad [2]$$

where $w(x)$ is the relative probability of use for the jth resource unit being selected at the ith choice for the predictor variables, x_i, and the β_i's are the coefficient estimates for each predictor variable.

I considered a total of 27 biologically relevant variables for possible inclusion in the fine-scale caribou use models, 13 of which were retained for model building. Eighteen *a priori* candidate models were developed using these covariates. These models were categorized into one of four groups: forage models, forest models, ground structure models and combination models. The top model in each of the first three groups was selected using AIC_c (Akaike's Information Criteria, corrected for small sample size bias; Burnham & Anderson 2002). The top performing model in each of these three subsets was then combined to produce the final group of models, which were subsequently evaluated using the methods outlined above.

3.3.2. Forage Occurrence Models

I evaluated the occurrence of a food resource relative to available forest cover attributes in a Design I approach (Taylor & Thomas 1990). I classified the food resource as occurring if its average percent cover in a plot was greater than its average cover at known caribou use sites. Covers less than this were classified as absences for my modelling purposes. I consider the average value to be a conservative estimate of what was biologically relevant, as no behavioural information was associated with caribou locations, i.e. I could not determine whether an animal was feeding, resting, or traveling at a given location.

Presence/absence data allowed me to develop resource selection probability functions (RSPF; Manly et al. 2002). RSPFs were obtained using logistic regression and model structure followed the form:

$$w^*(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_i x_i)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_i x_i)} \qquad [3]$$

where $w^*(x)$ is the resource selection probability function, β_0 is a constant, β_i are the selection coefficients for the x_i covariates.

A total of 14 biologically relevant variables were considered for inclusion in the candidate models. After univariate analysis, eight were retained for model building. Using these variables, I developed ten *a priori* candidate models. Model selection was again carried out using AIC_c and Akaike weights (Burnham & Anderson 2002). I used receiver operating characteristic (ROC) curves (Swets

1988) to validate the model and assess model fit. Model performance based on ROC scores can be grouped into three categories. Values ranging between 0.5 and 0.7 are considered to have low model accuracy; those between 0.7 and 0.9 are thought to have good model accuracy, while those above 0.9 indicate high model accuracy (Swets 1988).

3.3.3. Coarse-Scale Caribou Models

I used a case-control logistic regression to develop RSF models characterizing caribou habitat selection within the home range. Model structure followed the form shown in equation [2].

I considered a total of 30 biologically relevant variables for possible inclusion in the coarse-scale caribou occurrence models. After variable reduction 16 variables were retained as potentially important in distinguishing used and available sites. The GIS data layer of predicted forage resource occurrence was not included in the univariate variable reduction process.

I developed 15 *a priori* candidate models based on the remaining covariates. Model selection followed the information theoretic approach described above, but AIC, rather then AIC_c was used because the number of groups (n = 726) divided by the number of parameters in the largest model (15) was > 40 (Anderson et al. 2000).

I could not predict food resource occurrence across the entire landscape available to caribou because there was inadequate sampling in some habitat types. Therefore, this layer could not be incorporated into all models because locations

occurring where 'no data' were available for the forage resource layer were dropped from the analysis, rendering the log likelihoods incomparable. To address this, I chose to first model the relative probabilities of caribou occurrence independent of the forage resource layer, allowing me to use the full data set. Models identified through AIC procedures as having some support were re-run using a reduced data set (n = 600) both with and without the forage occurrence variable and applied only to the region where forage resource inference was possible. To allow for the maximum retention of use points, this analysis was run using 15 available points for every use point. Comparing the AIC values between models with and without the forage occurrence variable allowed me to assess whether the inclusion of this layer enhanced prediction of caribou occurrence on the landscape.

3.4. Multi-Model Inference

In cases where there is not strong support for the top model ($w_i < 0.9$) and coefficients are not stable across models, Burnham and Anderson (2002) suggest that model averaging should be used to produce more robust estimates and strengthen inference. The model averaging process incorporates uncertainty related to model selection and variable estimation within each candidate model.

When appropriate, I employed model averaging over a 90% confidence set based on w_i (Burnham & Anderson 2002). This method uses adjusted w_i ($w_{i\,adj}$) of the models in the candidate set to weight the coefficients, such that the w_i of the models included in the model averaging procedure are standardized to sum to 1.

Coefficients are averaged over all models in the candidate set in which they appear, so that $w_{i\,adj}$ may vary depending on the variable in question. The model-averaged estimate of a coefficient is calculated by multiplying the $w_{i\,adj}$ by the original coefficient and summing this value across all models in which the variable occurs. The standard errors are adjusted to this value.

3.5. Model Validation

In use/available study designs, the use site is not mutually exclusive from the distribution of available sites (Boyce et al. 2002). Site characteristics associated with use locations may be replicated in available sites leading to poor classification accuracy and making model validation through ROC curves inappropriate for these study designs (Boyce et al. 2002). Therefore, other validation methods were required for the coarse and fine-scale caribou habitat selection models.

I validated the fine-scale caribou models using a *k*-fold partitioning design (Fielding & Bell 1997). After fitting and identifying the best model, a testing to training ratio of 1:5 was chosen and the data were partitioned into five groups. I trained the model iteratively on four groups randomly chosen as training data. I validated each model, applying it to the remaining test group using the ranked bins of the predicted relative RSF values and a Spearman rank correlation statistic with $\alpha = 0.05$. In this instance the average Spearman rank correlation statistic indicates the within sample predictive ability of the model (Boyce et al. 2002).

Independent data were available with which to test the coarse-scale caribou occurrence model. The selected model was incorporated into a GIS framework (see below) and relative index of use surfaces were created for each year for which I had independent validation data. The validation points were applied to the appropriate binned relative index surface and assigned to the relative index bin in which they fell. As a measure of out-of-sample correspondence, the distribution of locations per bin was compared against that available using the Spearman rank correlation statistic ($\alpha = 0.05$).

3.6. Model Generalization

The generality of a model is determined by how well it predicts occurrence on areas outside that for which it was developed. The coarse-scale caribou occurrence model developed on the Narraway range was tested for generality on the Redrock-Prairie Creek (RPC) caribou range. The RPC range is adjacent to the Narraway range and caribou inhabiting both ranges are migratory mountain caribou. I applied the AIC-selected Narraway model (parameters and coefficients) to the available RPC landscape in a GIS framework. This was done over three consecutive years (2001-2003) and the relative index of use surfaces were calculated taking into account landscape change as a result of timber harvesting. Testing of the model was undertaken as described for model validation with independent data. Data from 23 female caribou in the RPC herd were used to test the generality of the Narraway model.

3.7. Spatial Interpolation

3.7.1. Forage Resource Occurrence

To spatially represent the probability of food resource occurrence, I determined the optimum cut-off value for the forage model derived through model averaging, maximizing both sensitivity and specificity, using an iterative process. Pixels with probability values below the cut-off were considered absent of the food resource while those above this point were considered to have the food resource present. The probability of food resource occurrence was only predicted over stands for which sufficient data were available. Stands where no inference as to the occurrence of the food resource was possible appear as 'no data.'

3.7.2. Coarse-Scale Caribou Occurrence

I incorporated the AIC-selected coarse-scale caribou model into a GIS framework, and produced a relative index surface of caribou occurrence. The surface was area-adjusted, and relative index of occurrence was assigned to 10 quantile bins, containing equal proportions. The relative index surface was not interpolated over the entire Narraway or RPC ranges because availability as I defined it did not cover the complete ranges. Because selection is dependent on availability, models applied to regions beyond their inference may generate unreliable estimates of selection (Garshelis 2000).

4. Results

4.1. Caribou Locations

Fine-scale caribou occurrence models were developed using data from six caribou (50 locations) collected during the winter of 2002-2003. Use sites sampled per caribou ranged from 5 to 15 with a mean of 8.3 sites per caribou. These data were pooled across individual caribou, assuming that, at a fine-scale, all adult female caribou select the same habitat attributes.

Coarse-scale caribou occurrence models were developed using data from 10 caribou (726 locations) collected over three winter seasons (2001-02, 2002-03 and, 2003-04; Figure 2.3). Two caribou followed in 2001-02 were also tracked in 2002-03. Because of the limited number of individuals collared, I pooled data across years and individuals. Table 2.1 shows the contribution of individual caribou and years to the model building process. I assumed all adult female caribou selected similarly with respect to stand level attributes. Data from an additional eight caribou were used for model validation. The average success rate of collar location acquisition for animals used in model building was 86% (GPS 1000 collars), and that of collars used for model validation was 78% (GPS 2200 collars).

4.2. Fine-Scale Caribou Habitat Selection

After the initial screening process, I retained 12 variables (Table 2.2) for use in the model building process (Table 2.3). Of the 18 candidate models evaluated, Model C4-15 was identified as the best model (Table 2.4). This model suggested that, at the 30 m plot level, caribou locations were associated with a higher percent cover of *C.*

mitis and *Stereocaulon spp.*, a greater component of tamarack, and with less coarse woody debris, bare ground, and shrubs > 10 cm. The model took the form

$$\hat{w}(x) = \exp[0.703\,(\%\ C.\ mitis) + 1.067\,(\%\ Stereocaulon\ spp.) + 0.040\,(\%\ \text{LT}) - 0.307\,(\%\ \text{CWD}) - 0.074\,(\%\ \text{shrubs} > 10\ \text{cm}) - 0.092\,(\%\ \text{bare ground})]$$

The low w_i (0.420; Table 2.4) and variability among common coefficients in the top models suggested the need to model average prior to making inference (Burnham & Anderson 2002).

Coefficients were averaged and standard errors adjusted over the 90% confidence set (Table 2.5). The averaged model on which inferences were based took the form:

$$\hat{w}(x) = \exp[0.739\,(\%\ C.\ mitis) + 0.931\,(\%\ Stereocaulon\ spp.) + 0.040\,(\%\ \text{LT}) - 0.306\,(\%\ \text{CWD}) - 0.070\,(\%\ \text{shrubs} > 10\ \text{cm}) - 0.094\,(\%\ \text{bare ground})]$$

Note that the structure of the model did not change due to the hierarchical nature of the 90% confidence set. Model averaged coefficients only changed slightly compared to the top model. Confidence intervals on all coefficients overlapped zero in both the top and averaged inference model, precluding strong inference based on coefficients. However, some trends are apparent based on the rankings associated with the sub-sets of models.

First, three of the four Combination models received the highest rankings. All three include a forage component in the form of percent cover of *C. mitis* and

Stereocaulon spp. Model 3 was ranked fourth and contains only the parameters *C. mitis* and *Stereocaulon spp.* These results suggest that these two lichen species are important in determining caribou habitat selection at a fine scale. Forage models (Models C4-1 – C4-6) generally ranked higher than the Ground Structure models (Models C4-12 – C4-14), which ranked higher than the Forest models (Models C4-7 – C4-11). Models containing tamarack (Models C4-8 & C4-10) ranked higher than comparable models containing pine (Models C4-7 & C4-9), although all models from the Forest sub-set had weak support, each having $w_i <$ 0.001. This suggests that at a fine scale, forest stand attributes were less important than forage and ground structure attributes.

K-fold cross validation on the averaged model revealed a high positive correlation across relative probability bins (mean $r_s = 0.913$, $P < 0.05$; Table 2.6), indicating that the model was robust and accurately predicted the data.

4.3. Forage Occurrence Model

Of the forage resources available and measured, *C. mitis* and *Stereocaulon spp.* were determined to be influential in determining fine-scale caribou selection. Unfortunately data limitations prevented me from modelling *Stereocaulon spp.* occurrence at the stand level. While *Stereocaulon spp.* has been identified as a potentially important forage species in alpine areas (Johnson et al. 2004a), it is considered unpalatable to caribou elsewhere (Thomas et al. 1996). Thus, I only modelled the occurrence of *C. mitis* relative to stand level attributes. All top fine-scale caribou models contained *C. mitis* (See 2.4.2) and there is considerable

support in the literature suggesting this species is of particular importance to caribou as a forage item (Thomas et al. 1996; Schaefer 1996; Arseneault et al. 1997; Svihus & Holand 2000; Johnson et al. 2003; Johnson et al. 2004a).

The average percent cover of *C. mitis* at known caribou use sites (1.31%) was significantly higher than at associated random sites (0.60%; $Z_{U\,0.05(1)} = 3.151$, $P < 0.001$). I therefore used 1.31% *C. mitis* cover as the cut-off value, above which it was classified as occurring and below which it was considered absent, from a caribou foraging perspective. This classification provided the binary dependent variable necessary for logistic regression.

Eight variables were retained (Table 2.7) for use in constructing the candidate model set for predicting *C. mitis* occurrence at the stand level (Table 2.8). Of the ten models evaluated, Model F3-10 was selected as the top model by virtue of its w_i (Table 2.8). *C. mitis* occurrence was associated with less rugged terrain in forest stands of moderate canopy closure, with a greater component of black spruce, a smaller component of white spruce and tamarack, and areas closer to seismic lines and water sources than sites where *C. mitis* did not occur. The model took the form:

$$\hat{w}^*(x) = \exp[-0.617 + 0.047(\text{canopy}) - 0.001(\text{canopy}^2) - 0.100(\%\,\text{SW}) + 0.006(\%\,\text{SB}) - 0.193(\%\,\text{LT}) - 1.054(\text{dist_wa}) - 0.433(\text{dist_si}) - 5.980(\text{TRI})].$$

Of the variables contained in this model, only the confidence intervals for dist_wa did not overlap zero, suggesting it has the strongest influence on *C. mitis* occurrence at this scale. The low w_i (0.504; Table 2.9) and variability among

common coefficients in the top models suggested the need to model average prior to making inference (Burnham & Anderson 2002).

Coefficients were averaged and standard errors adjusted over the 90% confidence set (Table 2.10). The averaged model on which inferences are based takes the form:

$$\hat{w}^*(x) = \exp[-1.170 + 0.049(\text{canopy}) - 0.001(\text{canopy}^2) - 0.110(\%\,\text{SW}) + 0.005(\%\,\text{SB}) - 0.202(\%\,\text{LT}) - 1.054(\text{dist_wa}) - 0.433(\text{dist_si}) - 5.980(\text{TRI})].$$

Note that because the top model contained all available variables, the structure of the model did not change. Although the coefficients change slightly compared to the top model, the direction of selection remained the same for all covariates. Model averaging increased the detected importance of % SW (95% CI don't overlap zero). Dist_wa remains influential in determining the distribution of *C. mitis*. The ROC score associated with the inference model was 0.724, indicating good model accuracy (Swets 1988). The probability cut-off for the predicted occurrence of *C. mitis* was determined to be 0.075, and resulted in a classification accuracy of 67.35%. The cut-off value was used to produce a predictive map of *C. mitis* occurrence (Figure 2.4).

4.4. Coarse-Scale Caribou Occurrence Model

The variables distance to edge, distance to anthropogenic edge, distance to linear feature, and the proportion of the land base within 10 km classified as a cut block were excluded from model building due to collinearity. The variable set was reduced to 14 after univariate analysis (Table 2.11), and these were used to

construct the 15 *a priori* candidate models (Table 2.12). These 15 models were tested using the full data set and Model C3-12 (Table 2.13) was the best predictor ($w_i = 0.823$). At this scale, caribou locations were associated with patches that were larger, and had a higher area to perimeter ratio, with stands that had a higher component of black spruce and a smaller component of fir, with less rugged terrain, greater distances from cut blocks but closer to seismic lines, and had a higher density of linear features within 10 km^2 than random points. The model took the form:

$$\hat{w}(x) = 0.073(\text{hab_are}) + 5.682(\text{hab_apr}) - 0.025(\%\ \text{FR}) + 0.005(\%\ \text{SB}) - 3.628(\text{TRI}) - 0.363(\text{dist_si}) + 0.077(\text{dist_cb}) + 0.011(\text{den_ln}).$$

All variables in this model are important contributors to the prediction of caribou occurrence at this scale, as none of their confidence intervals overlap zero. The relatively high w_i associated with this model and the stability of the coefficients across models precluded the need to model average (Burnham & Anderson 2002). This model was incorporated into a GIS framework, producing an annual relative index of caribou occurrence surface (Figure 2.5). There was a significant positive correlation between the predicted relative index of use by caribou and the occurrence of use locations from independent data sets (average: $r_{(s)} = 0.796$, $P < 0.010$; Table 2.14; Figure 2.6).

To assess the effect of the *C. mitis* probability layer, I added this layer to the top two models (C3-12 and C3-15). Models were re-evaluated using the

reduced data set. Model C3-12 with the *C. mitis* occurrence layer was selected as the top model with a w_i of 0.979 (Table 2.15), and took the form:

$$\hat{w}(x) = -0.044(\text{hab_are}) + 5.712(\text{hab_apr}) + 0.005(\%\ \text{FR}) + 0.004(\%\ \text{SB}) - 3.099(\text{TRI}) - 0.193(\text{dist_si}) + 0.071(\text{dist_cb}) + 0.014(\text{den_ln}) + 5.954(\text{prob_mitis}).$$

This model suggest that caribou selected smaller habitat patches with a higher area to perimeter ratio, stands that have a higher component of black spruce and fir, less rugged terrain, areas further from cut blocks but closer to seismic lines, have a higher density of linear features within 10 km^2, and occur in areas that have a higher predicted probability of *C. mitis* occurrence then random points. Variables hab_apr, % SB, TRI, den_ln, and prob_mitis had confidence intervals not overlapping zero, indicating they were strong contributors to the model.

The addition of the *C. mitis* predictive layer to the coarse-scale caribou occurrence models substantially improved model fit, as evidenced by the decline in AIC values when comparing models with and without the variable (Table 2.15), but did little to alter the distribution of areas where caribou were more likely to occur (Figure 2.7). Overall improvement is also evident through the validation process. Model 12 including *C. mitis* was marginally better than the model developed on the full data set, having an average $r_{(s)} = 0.818$, $P < 0.010$ (Table 2.16; Figure 2.8).

4.5. Model Generalization

I applied the AIC-selected coarse-scale caribou occurrence model, without the predicted *C. mitis* layer (C3-12) to the RPC caribou range. The Narraway model predicted caribou occurrence on the RPC range well in two of the three years tested (2001 & 2003), indicated by a significant positive Spearman rank correlation (Table 2.17, Figure 2.9). However in 2002, caribou locations were negatively correlated with the predictive surface generated by the Narraway model (Table 2.17, Figure 2.9). As a result, the Narraway model did not perform well overall on the RPC range (mean $r_s = 0.438$, $P < 0.500$; Table 2.17).

A comparison of the selection ratios on the two ranges for concurrent years is shown in Figure 2.10. The selection ratio adjusts the assigned rankings relative to the amount of area represented by each bin and is the basis for the Spearman rank test. Interestingly, in the winter of 2000-2001, the Narraway model appears to generalize quite well on the RPC range, having a higher Spearman Rank correlation then does the validation data from the Narraway range (Figure 2.10). However the observed trend is not as strong as that seen in the Narraway. This is not reflected in the Spearman rank statistic. Compare this to the data from the winter of 2002-2003, where the model predicted well and the trend was consistent across ranges (Figure 2.10).

5. Discussion

In west-central Alberta, all caribou winter ranges are subject to timber harvest as well as increasing pressures from the oil and gas sectors. The identification of

specific habitat requirements is crucial to the successful integration of caribou conservation strategies and sustainable land use management practices. This work represents the first attempt to model woodland caribou habitat selection on the Narraway winter range, the least developed of the four west-central Alberta caribou ranges. The information presented represents critical baseline data and provides a yardstick against which the effect of future development can be measured.

My primary objectives were to model caribou occurrence on the Narraway winter range at coarse (selection within the home range) and fine (selection of forage items) scales. Models at both scales validated well, with caribou distribution at the fine-scale being influenced by the occurrence of *C. mitis,* and *Stereocaulon spp.* At the larger scale caribou distribution was best explained by a combination of patch matrixes, stand composition, terrain and, anthropogenic variables. Overall, model performance was improved by incorporating the probability of *C. mitis* occurrence as a covariate in the coarse-scale model.

The fine-scale caribou models, representing the selection of forage items, did not reveal strong selection for specific forage species by caribou. However, an increase in sample size might result in improved parameter inference. In addition, the improvement seen in model fit with the inclusion of the *C. mitis* predictive layer in the coarse-scale occurrence model, suggests that this species in an important forage item on the Narraway range, as elsewhere (Thomas et al. 1996). *Stereocaulon spp.* also had support similar to that of *C. mitis*, appearing in all the top fine-scale models. Moreover, in comparing univariate models (Table

2.4, Models C4-4 & C4-5), the *Stereocaulon spp.* model outperformed the *C. mitis* model, even though it is not thought to be an important forage species (Thomas et al. 1996) except in alpine areas (Johnson et al. 2004a). Clearly the link between *Stereocaulon spp.* and caribou occurrence in this region requires additional investigation. Its prevalence at caribou use sites may be a reflection of the relatively low lichen cover in the Narraway (average: 6.03% $\pm$ 0.73 SE).

Some authors have recognized the importance of behaviour in governing resource use (Johnson et al. 2002b). The fine-scale plots I sampled were randomly chosen from used sites and may have included resting, traveling, and foraging sites. This likely contributed to the unstable nature of the coefficients across models and resulted in an inability to clearly identify important habitat attributes associated with fine-scale caribou selection. Identifying feeding areas through ground tracking (Johnson et al. 2002b; Szkorupa 2002) or fine scale movement modelling (Johnson et al. 2002a) to direct sampling might have led to more robust estimates.

Despite the difficulties in linking fine-scale habitat use to specific forage species, it was possible to model *C. mitis* occurrence at the stand level with reasonable fit and classification accuracy. While this layer did not significantly alter predicted caribou occurrence on the landscape (Figure 2.5 vs. Figure 2.7) it did help fine tune the model, enhancing the predictive abilities of the coarse-scale caribou occurrence model, particularly in 2002. This supports the assertion of Morrison (2001) that the inclusion of underlying mechanistic factors in habitat-based models will improve model performance. Unfortunately, inadequate

sampling and a greater diversity of stand types in the RPC made the application of the coarse-scale caribou occurrence model with the *C. mitis* predictive layer impossible. Thus I was not able to assess the effect of including this layer on the generality of the model. The ability to capture forage species in higher order models is critical to understanding the underlying mechanisms driving higher order selection (van Horne 1983; Morrison 2001) and may prove particularly useful when planning forest harvesting activities as caribou forage species can then be accounted for at the stand level, the scale at which management takes place.

On the Narraway range, *C. mitis* occurred in closer proximity to water than expected and was negatively correlated with the amount of white spruce in the canopy. Pine was not a strong predictor of *C. mitis* occurrence, as has been detected elsewhere (Rettie et al. 1997; Thomas et al. 1997; Szkorupa 2002). This may be in part related to the sampling strategy used here and my inability to adequately sample all habitat types. Although the relationship was weak, I found that *C. mitis* occurred closer than random to conventional seismic lines. This species is well suited to disturbed sites (Ahti & Oksanen 1990), and may have a competitive advantage in these areas compared to the undisturbed, feather moss dominated sites of the interior forest (Pharo & Vitt 2000).

The AIC-selected coarse-scale caribou occurrence model preformed well and accurately predicted caribou occurrence within the Narraway winter range. At this scale, caribou selected for larger forest patches with higher area to perimeter ratios and avoided cut blocks, reflecting selection for areas with little fragmentation (Bergerud & Page 1987; Bergerud 1990; Smith et al. 2000; James

& Stuart-Smith 2000). Caribou also selected for areas closer to conventional seismic lines and with higher linear densities. This is at odds with other findings (Oberg 2001; Dyer et al. 2001) but may in fact be a result of the predictive variables and analysis techniques I used. Dyer et al. (2001) showed that in northern Alberta, boreal caribou avoided seismic lines by a maximum distance of 100 m in the early winter and 250 m in the late winter, while Oberg (2001) did not find any effect of seismic lines on the distribution of mountain caribou in west-central Alberta during the winter months. Analyses from these studies applied a categorical buffering approach and compositional analysis (Aebischer et al. 1993). While I show caribou selected sites closer to seismic lines than random using a continuous measure of distance, this does not necessarily mean they occur frequently within the 100 m avoidance zone identified by Dyer et al. (2001). To investigate this, I conducted a post hoc compositional analysis similar to Dyer et al. (2001) and Oberg (2001) and found that while caribou selected for areas within 250 m of seismic lines, they avoided areas within 100 m of them. Caribou may be deflected from areas immediately surrounding seismic lines but still be closer to them than random locations. This situation has been documented in the arctic where barren ground caribou (*Rangifer tarandus groenlandicus*) have been displaced from areas adjacent to an oil field to more distal areas (Cameron et al. 1995).

The attraction to seismic lines also may be partially explained by the greater prevalence of lichens along these lines. This possibility highlights the necessity of linking habitat selection and population demographic models (van Horne 1983; Morrison 2001). Caribou may select to be closer to seismic lines due to increased

forage availability but be exposed to higher levels of predation risk (James & Stuart-Smith 2000; Smith 2004). Recent research from northern Alberta indicates that boreal caribou do not vacate their home ranges as a response to industrial activity (Tracz 2004), suggesting that caribou may not recognize the risk associated with staying in areas of high linear density, and thereby creating an ecological trap (Donovan & Thompson 2001; Delibes et al. 2001).

A second possibility is that the relationship between wolves and linear corridors documented by James and Stuart-Smith (2000) does not currently exist on the Narraway caribou range. The remoteness of the Narraway range limits human activity on seismic lines during the winter months. Without the packing of trails on seismic lines wolves may not benefit from traveling on them. Thus, the effect of conventional seismic lines on caribou mortality in this region may be minimal (Smith 2004). The Narraway caribou range supports only low numbers of moose (*Alces alces)*, elk (*Cervus elaphus*), and deer (*Odocoileus spp.*) (D. Hervieux, Alberta Sustainable Resource Development, pers. comm.). Therefore it is not likely to support a large population of wolves, translating into an inherently low risk of predation on the Narraway. There may be no need, at present, for caribou to avoid seismic lines to minimize their risk of predation (James & Stuart-Smith 2000). As industrial development on the landscape increases, and the amount of early seral forest increases, this relationship will undoubtedly change (Bergerud & Ballard 1988; Edmonds 1988; Cumming 1992; Rettie & Messier 2000). The community response to changing forest structure should be monitored to clearly document population level responses.

Noticeably absent from the coarse-scale caribou models was pine, however this does not mean that pine forests are not important habitat for caribou, as shown by numerous earlier studies (Edmonds 1988; Rettie et al. 1997; Szkorupa 2002; Johnson et al. 2003). Rather, selection for pine forests likely occurred at a higher order than investigated in this study. Habitat selection at finer scales may mask that of coarser scales (Johnson 1980; Thomas & Taylor 1990). For example, if selection for pine forests takes place at the level of the home range, then this habitat type will be abundant throughout the range and may not be selected for at finer scales.

While comprehensive comparisons between the selected coarse-scale model developed on the full data set and that developed with the inclusion of *C. mitis* on the reduced data set are not possible, the general pattern of selection was consistent over both models. However, four variables: patch size, prevalence of fir, distance to cut block, and distance to seismic line went from being strong predictors of caribou occurrence to having no significant effect. I do not attribute this change to the *C. mitis* layer per se, but rather to removal of the data points that fell beyond the scope of inference of the *C. mitis* layer. A number of the removed points fell in a unique portion of the winter range dominated by a remote alpine ridge surrounded by a sub-alpine fir forest. This area was used extensively by only one of the ten collared caribou. Removal of these data points reduced the contrast in the covariates, and likely impacted the coefficients in my models. This effect challenges the assumption that all caribou select for the same stand level attributes and questions the appropriateness of pooling data across individuals at this scale. While individual variation is important and reflects plasticity, for example in

forage acquisition or predator avoidance strategies (Gustine 2005), management cannot be expected to occur at the level of the individual. A general, validated model produced by pooling individuals is therefore appropriate for management, as it represents selection by the average animal. If the model validates well, as was this case in this study, then this average is assumed to adequately represent the population (Aebischer et al. 1993).

Although the stand level model generally predicted well on the Narraway it did not, on average, perform well on the RPC caribou range. Additionally, there was variation in model performance over years on both ranges. These results support the assertion of Manly et al. (2002), that inferences are limited temporally and spatially to the region of model development. Because of the dependent nature of the available points on the use sites, it was inappropriate to include year as a fixed effect in the models because there was no variation among years within groups. Sample size did not permit modelling selection by individual caribou on a yearly basis. Given that a decline in model performance was seen on both ranges in the same year, a factor operating at a larger scale than I observed may have had a major influence on selection in 2002. Weather patterns may affect habitat selection over large areas. Unfortunately, data on snow depth and condition, which are known to influence habitat selection by caribou (Szkorupa 2002), were not available for this study. Poor model performance in 2002 may be a reflection of a problem common to occurrence models: they are efficient at identifying habitat characteristics regularly selected

but may overlook others used less frequently or under abnormal conditions, regardless of their importance (Garshelis 2000; Manly et al. 2002).

The apparent strong performance of the model in 2001 on both the Narraway and RPC ranges also raises the question of the appropriateness of using the Spearman rank test to evaluate model performance (Boyce et al. 2002). The histogram for the Narraway range in this year (Figure 2.10) looks as expected, with the selection ratio maximized in bin10, indicating that Narraway caribou are strongly selecting areas where the model predicted high occurrence values. This is reflected in the high positive correlation between caribou location and the relative index of occurrence surfaces ($r_s = 0.801$, $P < 0.010$). The correlation between RPC caribou locations and their relative index surfaces is also high and positive, exceeding that of the Narraway, in fact ($r_s = 0.842$, $P < 0.005$). However the selection pattern is less striking, with ratios more evenly spread across the bins. Clearly, the model is not predicting high quality habitat on the RPC range as well as it does on the Narraway, yet the Spearman rank statistic indicates greater correspondence. This result underscores the need to use multiple forms of validation, where possible, and cautions against naïve interpretation of analytical output.

Although habitat-based models such as those presented here can inform management decisions, they should be viewed as adaptive habitat models that must evolve and be re-evaluated as new knowledge and information is acquired. The landscape in which caribou exist is not static and caribou use of habitats can be expected to vary with changing environmental conditions (Gustine 2005).

Maximum benefit will be gained if these models are used as part of an adaptive management framework (Walters 1986), which also includes structured hypothesis testing, evaluation through monitoring, and adjustment over time. While these models represent habitat use patterns, there is no assessment made of habitat quality (van Horne 1983; Morrison 2001). Van Horne (1983) defines habitat quality as the relationship between population density, survival and, fecundity. While it is often assumed, the relationship between habitat selection and habitat quality is rarely evaluated (Morrison 2001) and future work should focus on linking population demographic parameters, such as those identified by Smith (2004) to specific habitats.

6. Management Implications

The multi-scale habitat selection models developed using resource selection functions provide valuable, spatially explicit relative probabilities of caribou occurrence to land managers, which can be incorporated into management plans. However, care must be taken when interpreting the results of these models, recognizing that they are sensitive to a number of parameters used to generate them, such as the number of locations sampled as well as individual variation in selection patterns. They should be regarded as one tool, and used in conjunction with all available information. I believe that great strides can be made in evaluation of the cumulative effects of landscape change by continuing to monitor caribou and reassessing their patterns of selection in response to natural variation in conditions, as well as anthropogenic changes. However, this option no longer

exists on many caribou ranges, because baseline data are scarce and anthropogenic landscape change continues at an ever-increasing rate. Nevertheless, these models show promise in their ability to identify areas of relative importance to caribou given future landscape scenarios, thus advancing conservation efforts by directing development to areas where effects can be minimized.

Table 2.1: Individual caribou and yearly contributions to coarse-scale winter (December 1 – April 30) habitat modelling on the Narraway range (2002-2004), in west-central Alberta. Data were pooled over both individual and year. Year refers to the date on January 1.

Year	Caribou ID	# Locations
2002	709	114
	710	37
	711	24
	712	49
	Subtotal	**224**
	Mean ± SE	**56.0 ± 20.0**
2003	710	26
	712	15
	715	113
	717	42
	722	27
	723	36
	Subtotal	**259**
	Mean ± SE	**43.1 ± 14.5**
2004	718	114
	730	129
	Subtotal	**243**
	Mean ± SE	**121.5 ± 7.5**
	TOTAL	**726**
	MEAN ± SE	**72.6 ± 13.0**

Table 2.2: Variables considered for fine-scale caribou habitat modelling on the Narraway winter range in west-central Alberta. Sampling reflected selection during the 2002-2003 winter season.

Variables	Description	*P*
Arboreal Lichen Class	Average arboreal lichen class	0.318
% *Cladina mitis*	Average % cover of *C. mitis*	0.003*
% *Cladina rangiferina*	Average % cover of *C. rangiferina*	0.118*
% *Cladina spp*	Average % cover of *Cladina spp*	0.014*
% *Cladonia spp*	Average % cover of *Cladonia spp*	0.225*
% *Cetraria spp*	Average % cover of *Cetraria spp*	0.258
% *Stereocaulon spp*	Average % cover of *Stereocaulon spp*	0.087*
% *Peltigera spp*	Average % cover of *Peltigera spp*	0.796
% Other Lichen Species	Average % cover of other lichen species	0.483
% Total Lichen species	Average total lichen % cover over	0.027*
% Moss	Average % cover of moss	0.695
% Forbs	Average % cover of forbs	0.757
% Grass	Average % cover of grass	0.512
% Sedge	Average % cover of sedge	0.581
% Shrubs < 10 cm	Average % cover of shrubs < 10 cm in height	0.681
% Litter	Average % cover of litter	0.996
% CWD	Average % cover of coarse woody debris	0.036*
% Bare Ground	Average % bare ground within the plot	0.121*
% Tree Bole	Average % ground cover occupied by tree boles	0.802
% Shrubs > 10 cm	Average % cover of shrubs > 10 cm in height	0.031*
Canopy [a]	Estimated canopy cover over the 30m plot	0.586*
Canopy^2	Canopy cover quadratic	0.208*
% PL	Proportion of trees that were pine	0.183*
% SB	Proportion of trees that were black spruce	0.286
% SW	Proportion of trees that were white spruce	1.000
% LT	Proportion of trees that were tamarack	0.170*
% FR	Proportion of trees that were fir	1.000

[a] Canopy cover was retained because it is necessary to include the base form of variables when polynomials are used.

* For variable reduction purposes, univariate case-controlled logistic regressions were carried out. Variables with $P \leq 0.25$ (*) were retained for use in fine-scale caribou model building.

Table 2.3: *A priori* candidate models used in assessing fine-scale habitat attributes associated with caribou use on the Narraway winter range in west-central Alberta. Sampling reflected selection during the 2002-2003 winter season.

Model #	Model Structure
FORAGE MODELS	
C4-1	% *C. mitis* + % *C. rangiferina* + % *Cladonia spp* + % *Stereocaulon spp*
C4-2	% *Cladina spp* + % *Cladonia spp* + % *Stereocaulon spp*
C4-3	% *C. mitis* + % *Stereocaulon spp*
C4-4	% *C. mitis*
C4-5	% *Stereocaulon spp*
C4-6	% Total Lichen
FOREST MODELS	
C4-7	% PL + Canopy + Canopy^2
C4-8	% LT + Canopy + Canopy^2
C4-9	% PL
C4-10	% LT
C4-11	Canopy + Canopy^2
GROUND STRUCTURE MODELS	
C4-12	% CWD + % Shrubs > 10 cm + % Bare Ground
C4-13	% CWD + % Shrubs > 10
C4-14	% CWD
COMBINATION MODELS	
C4-15	Model C4-3+ Model C4-10 + Model C4-12
C4-16	Model C4-3 + Model C4-10
C4-17	Model C4-3 + Model C4-12
C4-18	Model C4-10 + Model C4-12

Table 2.4: A comparison of fine-scale habitat models used to characterize locations of Narraway caribou on the winter range (2002-2003) in west-central Alberta. Models are ranked by Δ AIC_c values. Akaike weights (w_i) indicate the likelihood of the model being the best of those tested. K indicates the number of parameters in the model. Models indicated with an * were included in the model averaging procedure.

Model	K	AIC_c	Δ AIC_c	w_i	Model Rank
FORAGE MODELS					
C4-3	3	57.279	0.000	0.481	1
C4-5	2	59.061	1.783	0.197	3
C4-1	5	59.409	2.130	0.166	2
C4-4	2	60.359	3.080	0.103	4
C4-2	4	61.888	4.610	0.048	5
C4-6	2	66.817	9.538	0.004	6
FOREST MODELS					
C4-10	1	68.690	0.000	0.396	1
C4-9	1	69.534	0.844	0.260	2
C4-8	3	70.539	1.849	0.157	3
C4-11	2	71.186	2.496	0.114	4
C4-7	3	72.080	3.390	0.073	5
GROUND STRUCTURE MODELS					
C4-12	3	59.878	0.000	0.565	1
C4-13	2	60.535	0.658	0.407	2
C4-14	1	65.839	5.962	0.029	3
COMBINATION MODELS					
C4-15	6	51.335	0.000	0.495	1
C4-16	3	51.949	0.614	0.364	2
C4-17	5	53.918	2.582	0.136	3
C4-18	4	60.601	9.266	0.005	4
ALL MODELS					
C4-15*	6	51.335	0.000	0.420	1
C4-16*	3	51.949	0.614	0.309	2
C4-17*	5	53.918	2.582	0.116	3
C4-3*	2	55.012	3.677	0.067	4
C4-5	1	56.889	5.554	0.026	5
C4-1	4	56.934	5.598	0.026	6
C4-4	1	58.187	6.851	0.014	7
C4-2	3	59.521	8.186	0.007	8
C4-12	3	59.878	8.542	0.006	9
C4-13	2	60.535	9.200	0.004	10
C4-18	4	60.601	9.266	0.004	11
C4-6	1	64.645	13.309	0.001	12
C4-14	1	65.839	14.504	< 0.001	13
C4-10	1	68.690	17.354	< 0.001	14
C4-9	1	69.534	18.198	< 0.001	15
C4-8	3	70.539	19.203	< 0.001	16
C4-11	2	71.546	20.210	< 0.001	17
C4-7	3	72.080	20.744	< 0.001	18

Table 2.5: A comparison of coefficients (β), standard errors (SE) and confidence intervals (CI) between the AIC-selected model and those derived from multi-model inference for fine-scale caribou use prediction on the Narraway winter range in west-central Alberta (2002-2003).

	Top Model				Model Average			
			95% CI				95% CI	
Variable	β	SE	Upper	Lower	β	SE	Upper	Lower
C. mitis	0.703	0.487	-0.251	1.657	0.739	0.474	-0.191	1.669
Stereocaulon spp	1.067	0.570	-0.050	2.184	0.931	0.549	-0.144	2.006
Tamarack	0.040	0.040	-0.002	0.082	0.040	0.032	-0.022	0.102
Shrubs > 10 cm	-0.074	0.047	-0.624	0.010	-0.070	0.046	-0.160	0.021
CWD	-0.307	0.161	-0.166	0.018	-0.306	0.160	-0.620	0.008
Bare Ground	-0.092	0.101	-0.290	0.106	-0.094	0.100	-0.289	0.102

Table 2.6: Cross-validated Spearman rank correlations (r_s) between the fine-scale caribou relative probability bins, derived from the AIC-selected model from the Narraway caribou winter range in west-central Alberta (2002-2003), and the frequency of withheld probabilities.

Set	r_s	*P*
1	0.872	0.054
2	0.894	0.041
3	0.900	0.037
4	0.900	0.037
5	1.000	<0.001
Average	**0.913**	**0.034**

Table 2.7: GIS predictor variables considered for coarse-scale *Cladina mitis* occurrence modelling on the Narraway winter range in west-central Alberta. Vegetation data determining the presence or absence of *C. mitis* was carried out in 2002 and 2003. For variable reduction purposes, standard univariate logistic regressions were carried out. Variables with $P \leq 0.25$ (*) were retained for use in coarse-scale *C. mitis* candidate models. All variables were continuous.

Variable	*P*	Description	GIS Data Source
Elev (m)	0.347	Elevation at site	Digital Elevation Model (DEM)[b]
TRI	0.201*	Terrain Ruggedness Index	DEM Spatial Analyst calculation
Age (yr)	0.558	Stand age	Forest cover layer[c]
Age^2 (yr)	0.313	Stand age quadratic	Calculated from forest cover layer
Canopy (%)	0.148*	Stand density	Forest cover layer
$Canopy^2$ (%)	0.085*	Stand density quadratic	Calculated from forest cover layer
% PL	0.370	Proportion pine in stand	Forest cover layer
% SB	0.150*	Proportion black spruce in stand	Forest cover layer
% SE	0.262	Proportion Engelmann spruce in stand	Forest cover layer
% SW	0.047*	Proportion white spruce in stand	Forest cover layer
% LT	0.164*	Proportion tamarack in stand	Forest cover layer
% FR	0.820	Proportion fir in stand	Forest cover layer
Dist_si (km)	0.135*	Distance from site to nearest conventional seismic line	Spatial Analyst calculation
Dist_wa (km)[a]	0.017*	Distance from site to nearest water source	Spatial Analyst calculation

[a] Distance to closest permanent water source.
[b] DEM obtained from the National Topographic Data Base
[c] Forest cover data was provided by the British Columbia Ministry of Forests and Weyerhaeuser Company.

Table 2.8: *A priori* candidate models used in assessing coarse-scale habitat attributes associated with *C. mitis* occurrence on the Narraway caribou winter range in west-central Alberta. Sampling reflected occurrence in 2002 and 2003.

Model #	Model Structure
F3-1	% LT + Canopy + Canopy^2 + TRI + Dist_wa + Dist_si
F3-2	% SB + Canopy + Canopy^2 + TRI + Dist_wa + Dist_si
F3-3	% SW + Canopy + Canopy^2 + TRI + Dist_wa + Dist_si
F3-4	Canopy + Canopy^2 + TRI + Dist_wa + Dist_si
F3-5	Canopy + Canopy^2 + Dist_wa + Dist_si
F3-6	% SB + % SW + % LT + Canopy + Canopy^2
F3-7	% SW + Canopy + Canopy^2
F3-8	% SB + Canopy + Canopy^2
F3-9	% LT + % SB + Canopy + Canopy^2 + Dist_wa
F3-10	% SB + % SW + % LT + Canopy + Canopy^2 + TRI + Dist_wa + Dist_si

Table 2.9: A comparison of candidate models used to characterize *C. mitis* occurrence in 2002 and 2003 on the Narraway caribou winter range in west-central Alberta. Models are ranked by Δ AIC$_c$ values. Akaike weights (w_i) indicate the likelihood of the model being the best of those tested. K indicates the number of parameters (including intercept) in the model. Model indicated with an * were included in the model averaging procedure.

Model #	K	AIC$_c$	Δ AIC$_c$	w_i	Model Rank
F3-10*	9	288.743	0.000	0.504	1
F3-6*	6	288.898	0.155	0.467	3
F3-3	7	295.329	6.586	0.019	2
F3-7	4	297.229	8.486	0.007	4
F3-1	7	300.407	11.664	0.001	5
F3-8	6	301.272	12.529	0.001	6
F3-4	6	305.996	17.253	< 0.001	7
F3-5	5	307.278	18.534	< 0.001	8
F3-2	7	307.559	18.816	< 0.001	9
F3-9	4	313.793	25.050	< 0.001	10

Table 2.10: A comparison of coefficients (β), standard errors (SE) and confidence intervals (CI) between the AIC selected model (F3-10) and those derived from multi-model inference for *C. mitis* occurrence prediction on the Narraway winter range, west-central Alberta (2002 & 2003).

	Top Model				Model Average			
			95% CI				95% CI	
Variable	**β**	**SE**	**Upper**	**Lower**	**β**	**SE**	**Upper**	**Lower**
Canopy	0.047	0.033	-0.018	0.112	0.049	0.033	-0.016	0.113
Canopy^2	-0.001	< 0.001	-0.001	< 0.001	-0.001	< 0.001	-0.001	< 0.001
% SW	-0.100	0.052	-0.201	0.002	-0.110	0.054	-0.215	-0.005
% SB	0.006	0.006	-0.006	0.018	0.005	0.006	-0.006	0.018
% LT	-0.193	0.103	-0.394	0.008	-0.202	0.104	-0.405	0.001
Dist_wa	-1.054	0.460	-1.957	-0.152	-1.054	0.460	-1.957	-0.152
Dist_si	-0.433	0.688	-1.781	0.915	-0.433	0.688	-1.781	0.915
TRI	-5.980	5.822	-17.391	5.432	-5.980	5.822	-17.391	5.432
INTERCEPT	-0.617	0.794	-2.172	0.939	-1.170	0.906	-2.945	0.606

Table 2.11: GIS predictor variables considered for coarse-scale caribou habitat modelling on the Narraway winter range in west-central Alberta. Univariate case-controlled logistic regressions were carried out and variables with $P \leq 0.25$ (*) were retained for use in candidate models. All variables are continuous.

Variable	*P*	Description	GIS Data Source
TRI	0.000*	Terrain Ruggedness Index	DEM Spatial Analyst calculation
Age (years)	0.085*	Stand age	Forest cover layer
Age^2 (years)	0.162*	Stand age quadratic	Calculated from forest cover layer
Canopy (%)	0.036*	Crown closure assigned to stand	Forest cover layer
Canopy^2 (%)	0.038*	Crown closure quadratic	Calculated from forest cover layer
% PL	0.574	Proportion pine in stand	Forest cover layer
% SB	0.000*	Proportion black spruce in stand	Forest cover layer
% SE	0.225*	Proportion engleman spruce in stand	Forest cover layer
% SW	0.000*	Proportion white spruce in stand	Forest cover layer
% LT	0.535	Proportion tamarack in stand	Forest cover layer
% FR	0.000*	Proportion fir in stand	Forest cover layer
Dist_si (km)	0.001*	Distance to nearest conventional seismic line	Spatial Analyst calculation
Dist_wa (km)[a]	0.299	Distance to nearest water source	Spatial Analyst calculation
Dist_we (km)	0.851	Distance to nearest well site	Spatial Analyst calculation
Dist_rd (km)	0.324	Distance to nearest road	Spatial Analyst calculation
Dist_cb (km)	0.109*	Distance to nearest cut block	Spatial Analyst calculation
Dist_ne (km)	0.044*	Distance to closest natural edge	Spatial Analyst calculation
Prop_cb	0.311	Proportion of land base in 1 km^2 that is classed as cut block	Spatial Analyst calculation
Den_lin (km/km^2)	0.373	Length of linear features within 1 km^2	Spatial Analyst calculation
Den_ln (km/10km^2)	0.002*	Length of linear features within 10 km^2	Spatial Analyst calculation
Hab_are (km^2)	0.000*	Area of patch defined by habitat	Calculated from forest cover layer
Hab_per (km)	0.711	Perimeter of patch defined by habitat	Calculated from forest cover layer
Hab_apr (km/km2)	0.000*	Area to perimeter ratio for patches defined by habitat	Calculated from forest cover layer
Edge_ar (km^2)	0.857	Area of patch defined by edge	Calculated from forest cover layer
Edge_pe (km)	0.472	Perimeter of patch defined by edge	Calculated from forest cover layer
Edge_ap (km/km^2)	0.075*	Area to perimeter ratio for patches defined by edge	Calculated from forest cover layer
Prob_mitis[b]		Estimated probability of *C. mitis* occurrence	RSPF calculation

[a] Distance to closest permanent water source.
[b] Prob_mitis was not included in the variable reduction process

Table 2.12: *A priori* candidate models used in assessing coarse-scale habitat attributes associated with caribou occurrence on the Narraway winter range in west-central Alberta. Sampling reflected winter occurrence of caribou from 2001-2004.

Model #	Model Structure
C3-1	% SB + Canopy + Canopy^2 + Age + Age^2
C3-2	% SW + Canopy + Canopy^2 + Age + Age^2
C3-3	% FR + Canopy + Canopy^2 + Age + Age^2
C3-4	Canopy + Canopy^2 + Age + Age^2 + TRI + Dist_ne + Hab_are + Hab_apr
C3-5	TRI + Dist_ne + Hab_are + Hab_apr
C3-6	% FR + TRI + Hab_are + Hab_apr
C3-7	Dist_si + Dist_cb + den_ln + TRI
C3-8	Hab_are + Age + Age^2 + Canopy + Canopy^2
C3-9	% SW + % SB + % SE + % FR + Age + Age^2 + Canopy + Canopy^2
C3-10	Hab_are + Hab_apr
C3-11	% FR + TRI + Hab_are + Hab_apr + Dist_ne
C3-12	% FR + % SB + TRI + Hab_are + Hab_apr + Dist_si + Dist_cb + Den_ln
C3-13	% FR + % SB + % SW + % SE + TRI + Hab_are + Hab_apr + Dist_ne + Age + Age^2 + Canopy + Canopy^2
C3-14	Dist_si + Dist_cb + den_ln
C3-15	% FR + % SB + % SW + % SE + TRI + Hab_are + Hab_apr + Dist_ne + Age + Age^2 + Canopy + Canopy^2 + Dist_ si + Dist_cb + Den_ln

Table 2.13: A comparison of candidate models used to characterize caribou occurrence on the Narraway winter range in west-central Alberta. Models are ranked by Δ AIC values. Akaike weights (w_i) indicate the likelihood of the model being the best of those tested. K indicates the number of parameters in the model. Sampling reflected winter caribou occurrence in 2001-2004.

Model #	K	AIC	ΔAIC	w_i	Model Rank
C3-12	8	4262.68	0	0.823	1
C3-15	15	4265.76	3.08	0.177	2
C3-13	12	4281.104	18.424	< 0.001	3
C3-11	5	4292.208	29.528	< 0.001	4
C3-6	4	4292.912	30.232	< 0.001	5
C3-4	8	4300.976	38.296	< 0.001	6
C3-5	4	4302.588	39.908	< 0.001	7
C3-10	2	4335.908	73.228	< 0.001	8
C3-8	5	4336.758	74.078	< 0.001	9
C3-9	8	4341.83	79.15	< 0.001	10
C3-3	5	4358.71	96.03	< 0.001	11
C3-7	4	4366.47	103.79	< 0.001	12
C3-14	3	4401.446	138.766	< 0.001	13
C3-2	5	4407.314	144.634	< 0.001	14
C3-1	5	4408.742	146.062	< 0.001	15

Table 2.14: The Spearman Rank correlations between independent caribou locations for the specified year and the appropriate coarse-scale relative index of use surface. The surface was developed from the AIC-selected model depicting winter habitat use by caribou (2001-2004) on the Narraway winter range in west-central Alberta and did not include *C. mitis* predictive layer.

Year	r_s	*P*
2001	0.806	0.005
2002	0.467	0.174
2003	0.957	< 0.001
2004	0.952	< 0.001
Average	**0.796**	**< 0.010**

Table 2.15: A comparison of coarse-scale models run on a reduced number of caribou locations from the Narraway winter range in west-central Alberta (2001-2004) with and without the predictive *C. mitis* layer. Models are ranked by Δ AIC values. Akaike weights (w_i) indicate the likelihood of the model being the best of those tested. K indicates the number of parameters in the model.

Model #	K	AIC	ΔAIC	w_i	Model Rank
C3-12 - with *C. mitis*	9	3218.272	0	0.979	1
C3-15 - with *C. mitis*	16	3225.958	7.686	0.021	2
C3-15	15	3265.228	46.956	< 0.001	3
C3-12	8	3279.204	60.932	< 0.001	4

Table 2.16: The Spearman Rank correlations between independent caribou locations for the specified year and the appropriate coarse-scale relative index of use surface. The surface was developed from the AIC-selected model depicting winter habitat use by caribou (2001-2004) on the Narraway winter range in west-central Alberta and included the *C. mitis* predictive layer.

Year	r_s	*P*
2001	0.830	0.003
2002	0.600	0.067
2003	0.925	< 0.001
2004	0.915	< 0.001
Average	**0.818**	**< 0.010**

Table 2.17: The Spearman Rank correlations between Redrock-Prairie Creek caribou winter locations (2001-2003) for the specified year and the appropriate coarse-scale relative index of use surface developed from the AIC-selected Narraway model (2001-2004). Both ranges are located in west-central Alberta.

Year	r_s	*P*
2001	0.842	0.002
2002	-0.442	0.200
2003	0.915	< 0.001
Average	**0.438**	**< 0.500**

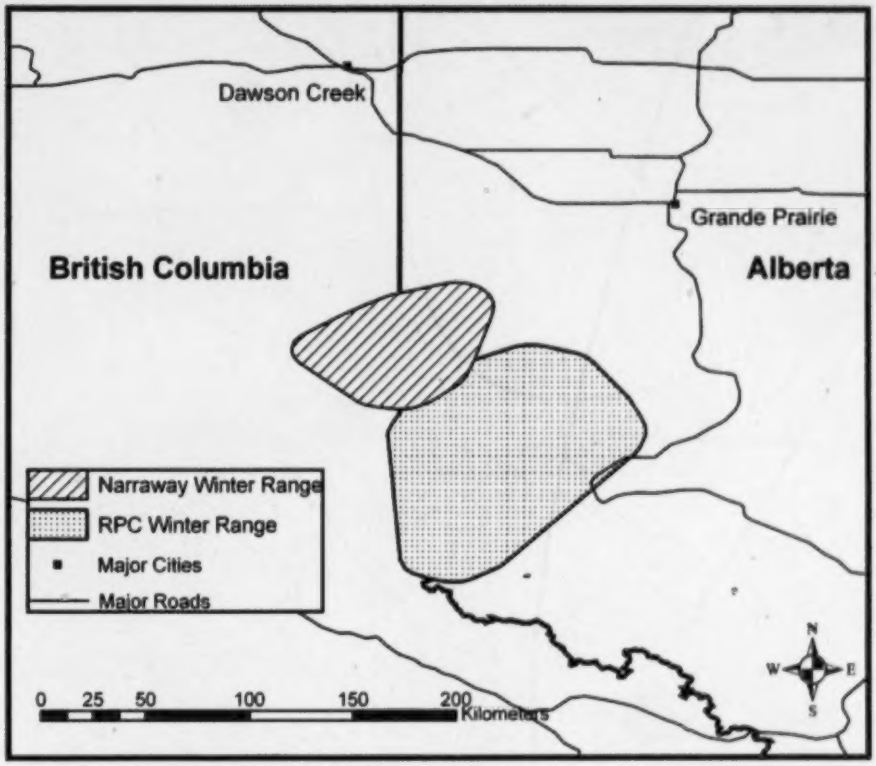

Figure 2.1: Location of the Narraway and Redrock-Prairie Creek winter caribou ranges in west-central Alberta.

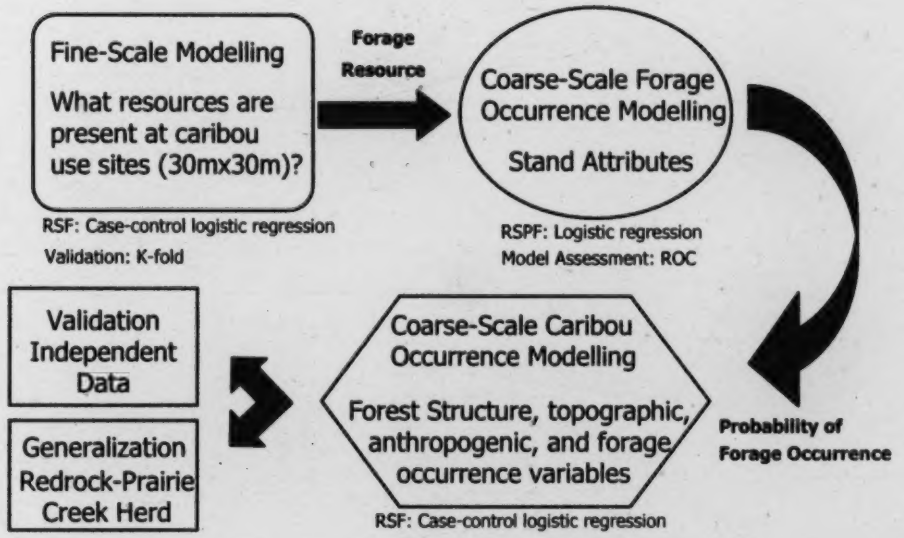

Figure 2.2: A conceptual diagram illustrating the modelling processes involved in determining coarse-scale attributes associated with caribou occurrence on the available Narraway winter range in west-central Alberta, Canada. Forage resources identified through fine-scale modelling as being important in determining caribou occurrence were extrapolated to the landscape level. The predictive surface generated from this process was then combined with other variables to predict the occurrence of caribou on the landscape. This coarse-scale caribou occurrence model was then validated using independent caribou data from the Narraway winter range and tested for generality on the Redrock-Prairie Creek caribou range.

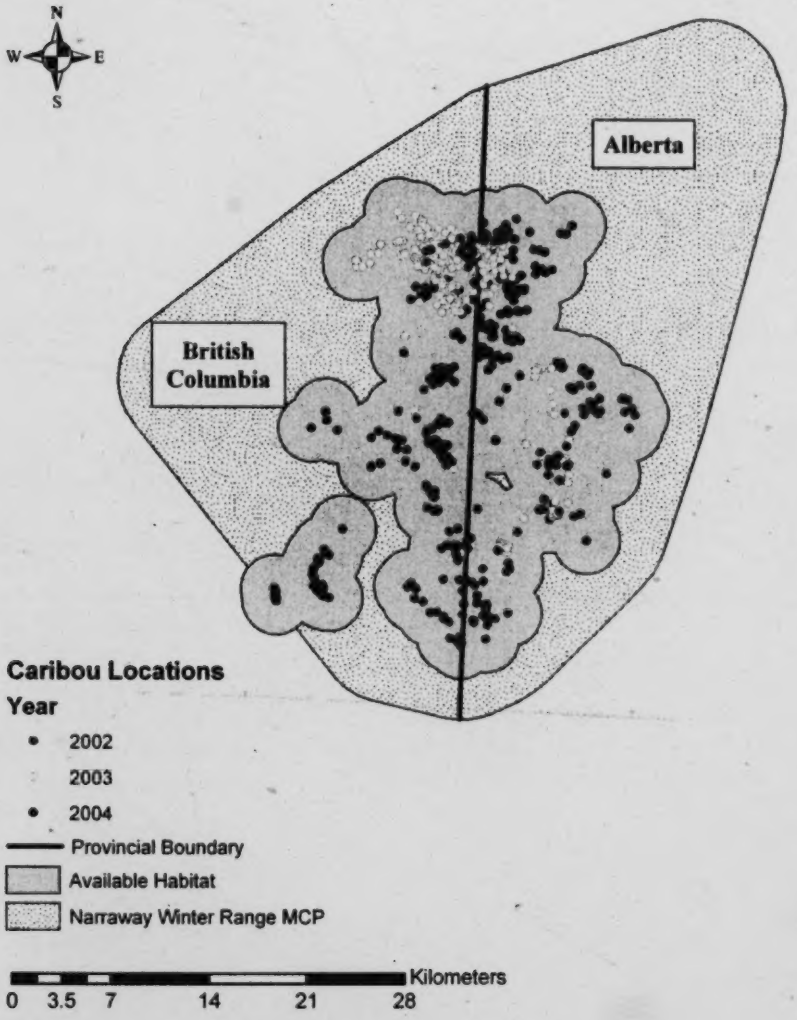

Figure 2.3: Winter caribou locations (2002-2004) used in the development of coarse-scale caribou occurrence models for the Narraway range in west-central Alberta. Note that data were pooled across individuals and years. Available habitat was defined by a 2.4 km buffer around individual use points, representing the 90th percentile of the daily distance traveled by all radio collared caribou.

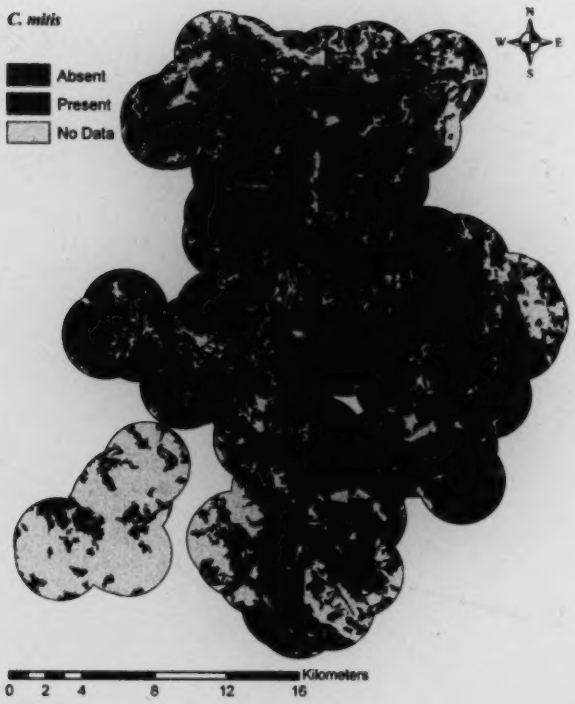

Figure 2.4: The predicted occurrence of the terrestrial lichen species *Cladina mitis* over the landscape available to caribou on the Narraway winter range in west-central Alberta. The map was produced using a model averaging approach over a 90% confidence set. A probability cut off of 0.075 was used to classify presence/absence. Grey regions in the map represent areas over which no inference was possible. The vertical line indicates the Alberta-British Columbia boundary.

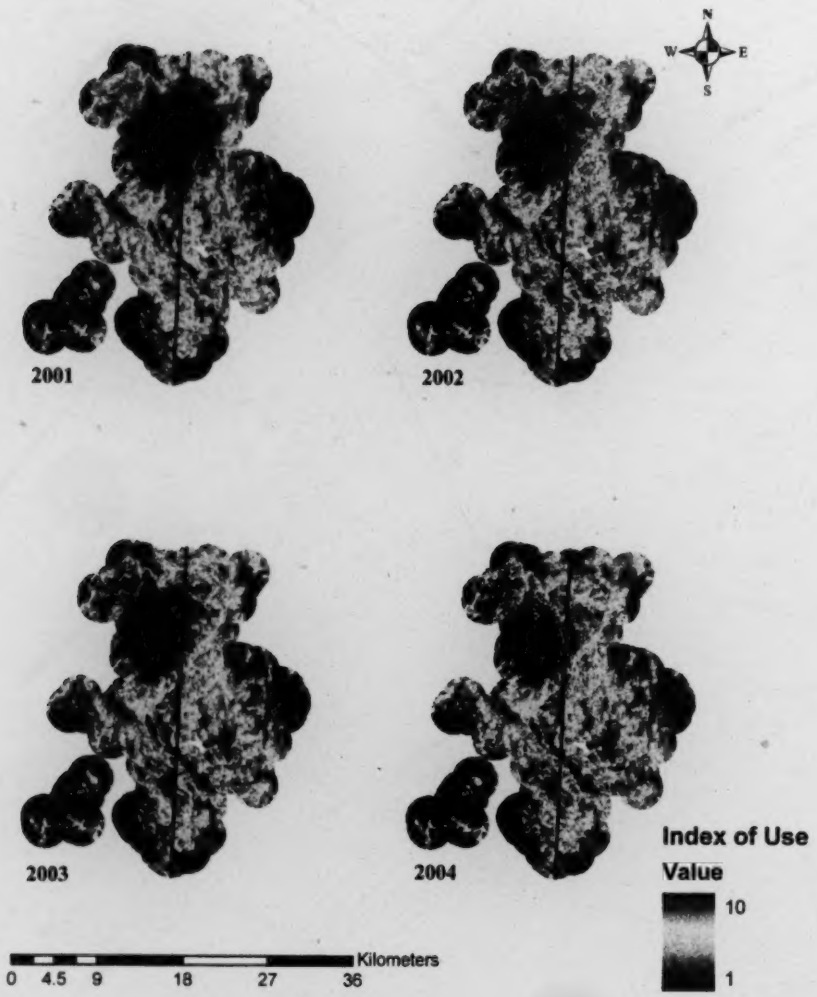

Figure 2.5: The relative index of caribou occurrence on the Narraway winter range in west-central Alberta (December 1 – April 30) using the AIC-selected coarse-scale caribou occurrence model (Model 12). The model was developed using location data from10 caribou, sampled from 2002 – 2004. Bins were area-adjusted, with pixels in Bin 10 reflecting areas where there was a high relative index of caribou occurrence and those in Bin 1 indicating areas where there was a low relative index of caribou occurrence. Years indicated reflect the date on January 1. The vertical line indicates the Alberta-British Columbia boundary.

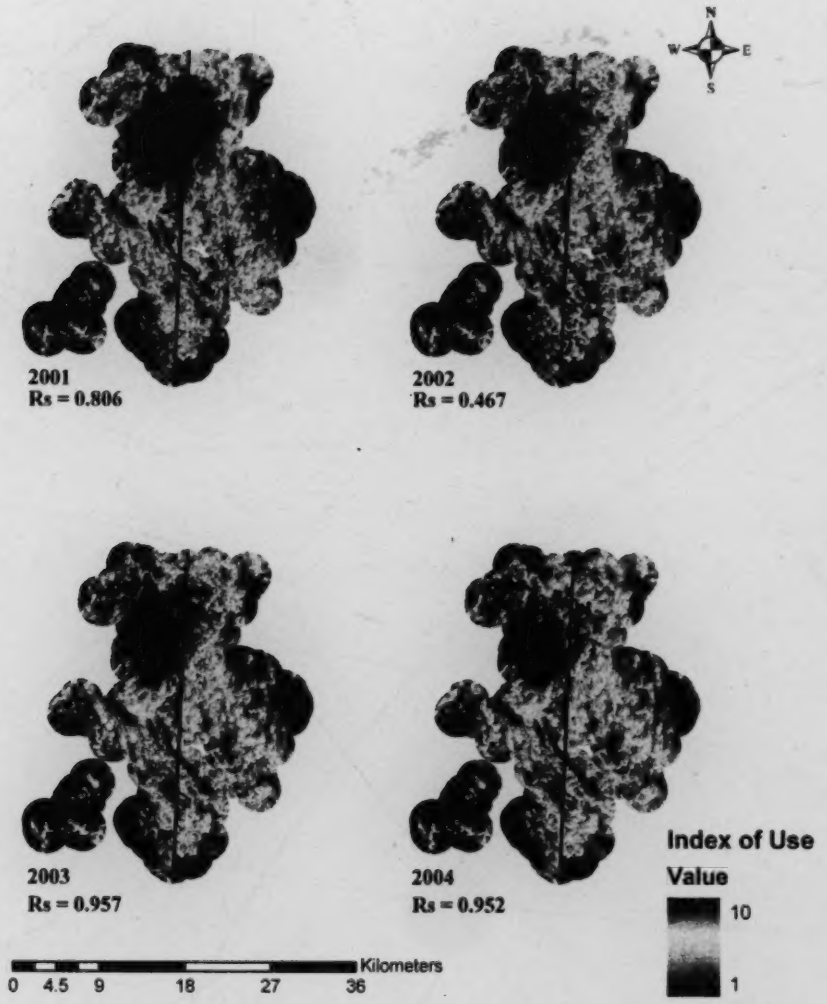

Figure 2.6: The location of the points used in the validation process overlaid on the relative index of caribou occurrence on the Narraway winter range in west-central Alberta (December 1 – April 30). Correlations between validation data and maps representing specific years are indicated on the figure. The average Spearman Rank correlation (Rs) over all four years was 0.796, $P < 0.010$. Years indicated reflect the date on January 1. The vertical line indicates the Alberta-British Columbia boundary.

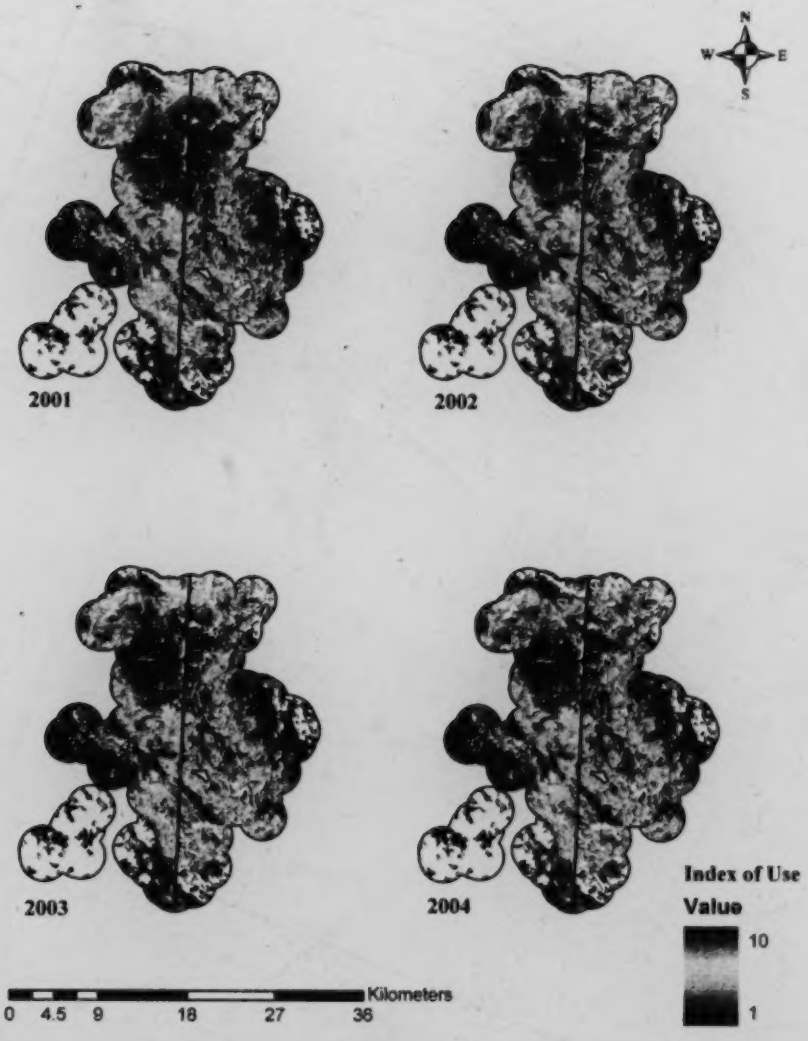

Figure 2.7: The relative index of caribou occurrence on the Narraway winter range in west-central Alberta (December 1 – April 30) using the AIC-selected coarse-scale caribou model that incorporated the probability of *Cladina mitis* occurrence. The model was developed using data from10 caribou sampled from 2002 – 2004. Bins were area adjusted, with pixels in Bin 10 reflecting areas where there was a high relative index of caribou occurrence and those in Bin 1 indicating areas where there was a low relative index of caribou occurrence. White areas are regions where inference as to the probability of *C. mitis* occurrence was not possible. Years indicated reflect the date on January 1. The vertical line indicates the Alberta-British Columbia boundary.

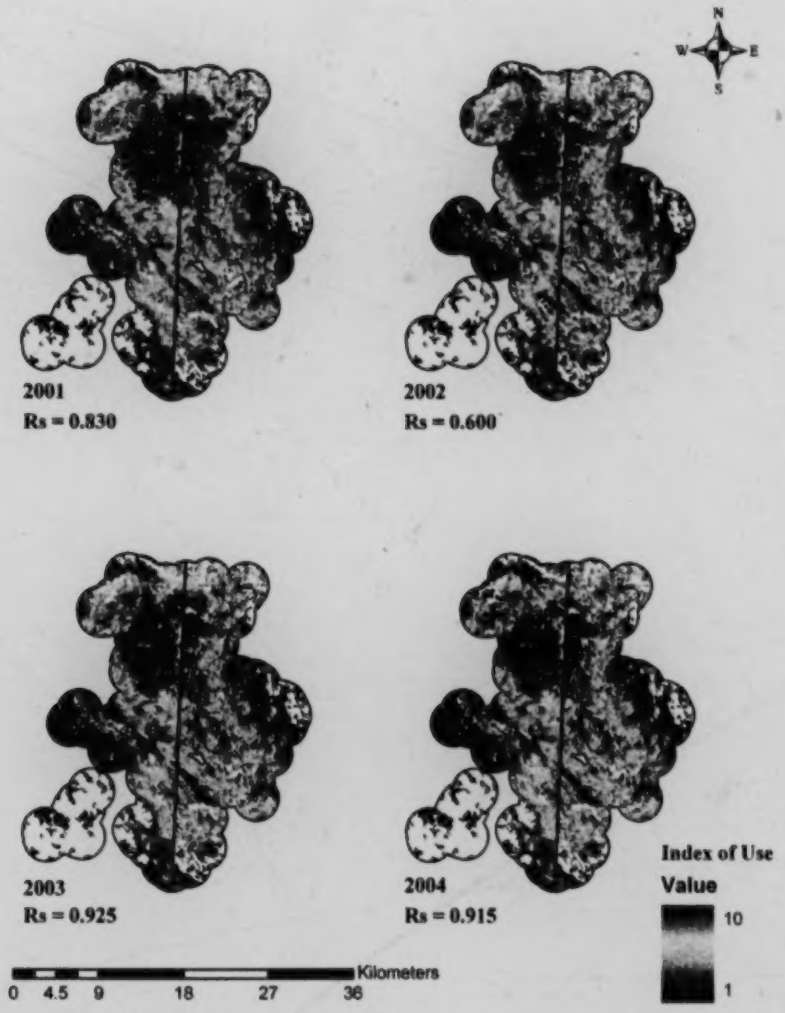

Figure 2.8: The location of points used in the validation process overlaid on the relative index of caribou occurrence on the Narraway winter range in west-central Alberta (December 1 – April 30). Index surfaces were produced using the AIC-selected coarse-scale caribou model that incorporated the probability of *Cladina mitis* occurrence. Correlations between validation data and index surfaces representing specific years are indicated on the figure. The average Spearman Rank correlation (Rs) over all four years was 0.818, $P < 0.010$. White areas are regions where inference as to the probability of *C. mitis* occurrence was not possible. Years indicated reflect the date on January 1. The vertical line down indicates the Alberta-British Columbia boundary.

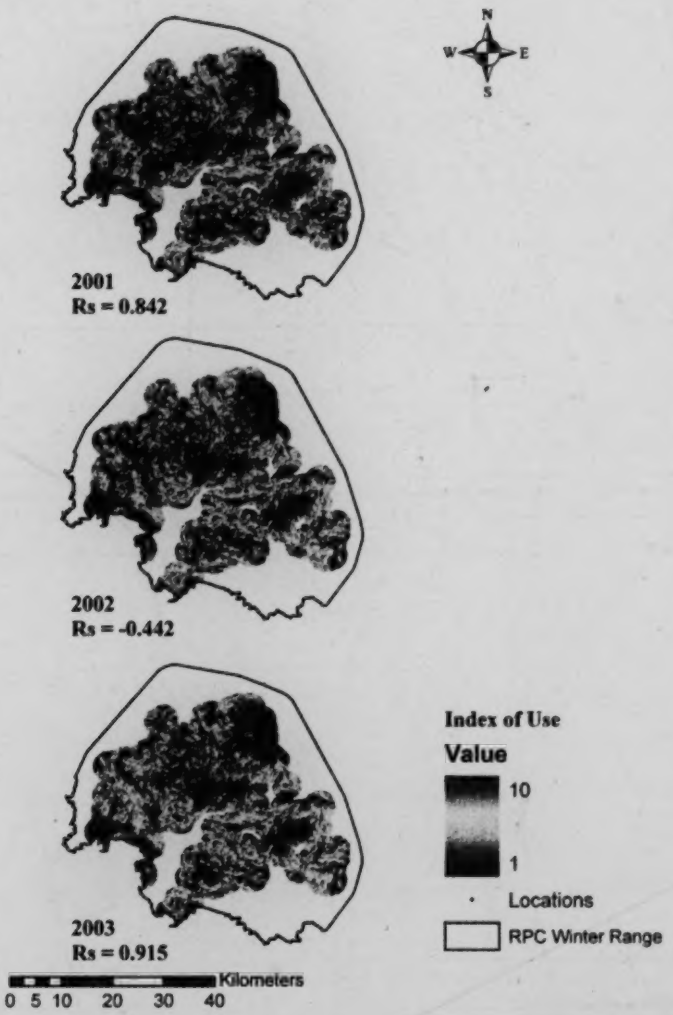

Figure 2.9: The relative index surface of caribou occurrence on the Redrock-Prairie Creek (RPC) winter range (December 1 – April 30) produced by applying the AIC-selected coarse-scale caribou model from the Narraway range (Model 12) to the RPC range. Both ranges are located in west-central Alberta. Bins were area adjusted with pixels in Bin 10 reflecting areas where there was a high relative index of caribou occurrence and those in Bin 1 indicating areas where there was a low relative index of caribou occurrence. Correlations between caribou locations used to test for generality and the probability surfaces for specific years are indicated on the figure. The average Spearman Rank correlation (Rs) over all three years was 0.438, $P < 0.500$. Years indicated reflect the date on January 1.

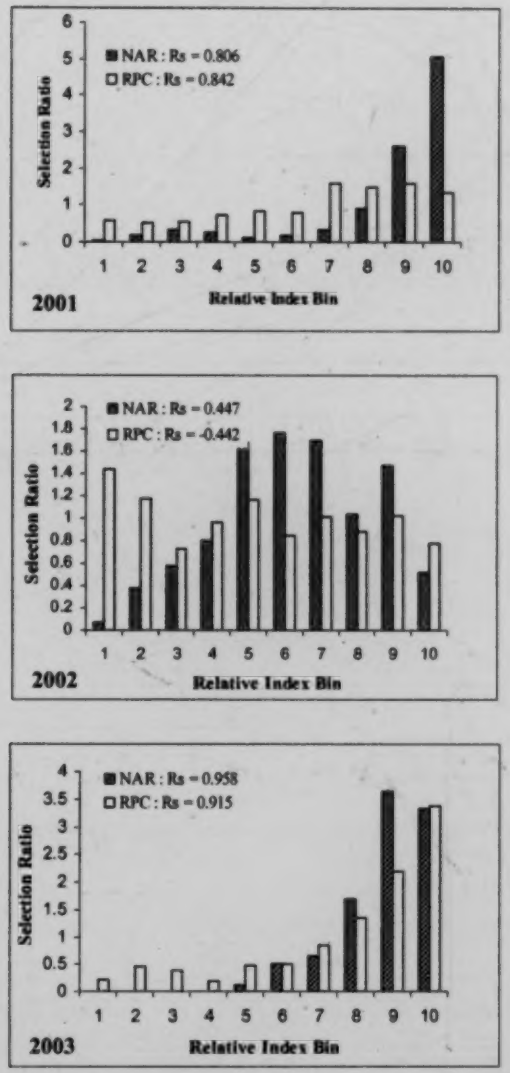

Figure 2.10: Selection ratios displayed by Narraway (NAR; independent data) and Redrock-Prairie Creek (RPC) caribou for area-adjusted relative index bins. Bins were derived from the relative index surface developed using the AIC-selected model for coarse-scale caribou selection on the Narraway winter range (Dec.1 – Apr. 30). Spearman Rank correlation (Rs) values are indicated. Note the apparently good performance of the Narraway model on the RPC range in 2001, the poor performance of the model on both ranges in 2002 and, the strong performance of the model on both ranges in 2003. Years indicated reflect the date on January 1.

7. Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio- tracking data. Ecology **74**:1313-1325.

Ahti, T., and J. Oksanen. 1990. Epigeic lichen communities of taiga and tundra regions. Vegetatio **86**:39-70.

Alberta Energy. 1996. IL 96-7 Procedural guide for oil and gas activity on caribou range. Government of Alberta. URL: http://www.energy.gov.ab.ca/room/updates/letters/1996/96-07.htm [Revision date: 14 May 1998].

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management **64**:912-923.

Armleder, H. M., S. K. Stevenson, and S. D. Walker. 1992. Estimating the abundance of arboreal forage lichens. B.C. Ministry of Forests. Victoria, BC.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology **77**:215-227.

Arseneault, D., N. Villeneuve, C. Boismenu, Y. Leblanc, and J. Deshaye. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Quebec: an application of fire history and Landsat data. Journal of Applied Ecology **34**:65-78.

Beckingham, J. D., and J. H. Archibald. 1996. Field guide to the ecosites of west-central Alberta. Canadian Forest Service, Northwest Region, Northern Forestry Centre, Edmonton, Alberta.

Bergerud, A. T. 1992. Rareness as an antipredator strategy to reduce predation risk for moose and caribou. *In*: Wildlife 2001: populations. D.R. McCullough and R.H. Barrett, *eds*. Elsevier Applied Science, New York, NY. USA. Pp 556-581.

Bergerud, A. T., and W. B. Ballard. 1988. Wolf predation on caribou - the Nelchina herd case-history, a different interpretation. Journal of Wildlife Management **52**:344-357.

Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology **65**:1597-1606.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281-300.

Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. Journal of Wildlife Management **61**:1127-1133.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, Inc. New York, New York, USA.

Cameron, R. D., E. A. Lenart, D. J. Reed, K. Whitten, and W. T. Smith. 1995. Abundance and movements of caribou in the oilfield complex near Prudhoe Bay, Alaska. Rangifer **15**:3-7.

Chamberlain, T. C. 1965. The method of multiple working hypotheses. Science **148**:754-759.

Chatterjee, S., A. S. Hadi, and B. Price. 2000. Regression analysis by example. 3rd Edition. John Wiley & Sons, Inc. New York, New York, USA.

Cichowski, D. B. 1993. Seasonal movements, habitat use, and winter feeding ecology of woodland caribou in west-central British Columbia. B.C. Ministry of Forests Land Management Report Number 79.

Compton, B. W., J. M. Rhymer, and M. Mccollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology **83**:833-843.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology **80**:566-575.

Cumming, H. G. 1992. Woodland caribou - facts for forest managers. Forestry Chronicle **68**:481-489.

D'eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin **30**:430-439.

Delibes, M., P. Gaona, and P. Ferreras. 2001. Effects of an attractive sink leading into maladaptive habitat selection. American Naturalist **158**:277-285.

Donovan, T. M., and F. R. Thompson. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications **11**:871-882.

Dyer, S. J., J. P. O'neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management **65**:531-542.

Edmonds, E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. Canadian Journal of Zoology **66** :817-826.

Erickson, W. R., T. L. McDonald, K. G. Jerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. *In*: Radio tracking and animal populations. J. J. Millspaugh and J. M. Marzluff, *eds.* Academic Press, New York, NY. USA. Pp 211-242.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. *In*: Research techniques in animal ecology: consequences and controversies. L. Boitani and T. K. Fuller, *eds*. Columbia University Press, New York, NY. USA. Pp 111-164.

Gustine, D. D. 2005. Plasticity in selection strategies of woodland caribou (*Rangifer tarandus caribou*) during winter and calving. MSc. Thesis. University of Northern British Columbia, Prince George, British Columbia, Canada.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. John Wiley & Sons, Inc. New York, New York, USA.

James, A. R. C., S. Boutin, D. M. Herbert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management **68**:799-809.

James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management **64**:154-159.

Johnson, C. J., N. D. Alexander, R. D. Wheate, and K. L. Parker. 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. Forest Ecology and Management **180**:241-248.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002a. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology **71**:225-235.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002b. A multiscale behavioural approach to understanding the movements of woodland caribou. Ecological Applications **12**:1840-1860.

Johnson, C. J., K. L. Parker, D. C. Heard, and D. R. Seip. 2004a. Movements, foraging habits, and habitat use strategies of northern woodland caribou during winter: Implications for forest practices in British Columbia. BC Journal of Ecosystems and Management **5**:22-35.

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004b. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology **41**:238-251.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**:65-71.

Jones, N. E., and W. M. Tonn. 2004. Resource selection functions for age-0 arctic grayling (*Thymallus arcticus*) and their application to stream habitat compensation. Canadian Journal of Fisheries and Aquatic Science **61**:1736-1746.

King G., and L. Zeng. 2001. Logistic regression in rare events data. Political Methodology **12**:137-163.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.

McLoughlin, P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management **67**:755-761.

Menard, S. 1995. Applied logistic regression analysis. Sage University Paper Series on Quantitative Applications in the Social Sciences, 07-106. Sage Publications. Thousand Oaks, California, USA.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great-Lakes region. Conservation Biology **9**:279-294.

Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management **65**:613-623.

Nellemann, C., and R. D. Cameron. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology **76**:1425-1430.

Nellemann, C., and G. Fry. 1995. Quantitative-analysis of terrain ruggedness in reindeer winter grounds. Arctic **48**:172-176.

Nielsen, S. E., R. H. M. Munro, E. L. Bainbridge, G. B. Stenhouse, and M. S. Boyce. 2004. Grizzly bears and Forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. Forest Ecology and Management **199**:67-82.

Oberg, P. R. 2001. Responses of mountain caribou to linear features in a west-central Alberta landscape. MSc Thesis, University of Alberta, Edmonton Alberta, Canada.

Pendergast, J. F., S. J. Gange, M. A. Newton, M. J. Lindstrom, M. Palta, and M. R. Fisher. 1996. A survey of methods for analyzing clustered binary response data. International Statistics Review **64**:89-118.

Pharo, E. J., and D. H. Vitt. 2000. Local variation in bryophyte and macro-lichen cover and diversity in montane forests of western Canada. Bryologist **103**:455-466.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography **23**:466-478.

Rettie, W. J., J. W. Sheard, and F. Messier. 1997. Identification and description of forested vegetation communities available to woodland caribou: relating wildlife habitat to forest cover data. Forest Ecology and Management **93**:245-260.

Schaefer, J. A. 1996. Canopy, snow, and lichens on woodland caribou range in southeastern Manitoba. Rangifer, Special Issue **9**:239-244.

Schaefer, J. A., C. M. Bergman, and S. N. Luttich. 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology **15**:731-739.

Schaefer, J. A., and W. O. Pruitt. 1991. Fire and woodland caribou in Southeastern Manitoba. Wildlife Monographs **116**:1-39.

Smith, K. G. 2004. Woodland caribou demography and persistance relative to landscape change in west-central Alberta. MSc Thesis, University of Alberta, Edmonton Alberta, Canada.

Smith, K. G., E. J. Ficht, D. Hobson, T. C. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear- cut logging in west-central Alberta. Canadian Journal of Zoology **78**:1433-1440.

Stevenson, S. 1990. Managing second growth forests as caribou habitat. Rangifer, Special Issue **3**:139-144.

Svihus, B., and O. Holand. 2000. Lichen polysaccharides and their relation to reindeer/caribou nutrition. Journal of Range Management **53**:642-648.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science **240**:1285-1293.

Szkorupa, T. D. 2002. Multi-scale habitat selection by mountain caribou in west central Alberta. MSc Thesis, University of Alberta, Edmonton Alberta, Canada.

Terry, E. L., B. N. Mclellan, and G. S. Watts. 2000. Winter habitat ecology of mountain caribou in relation to forest management. Journal of Applied Ecology **37**:589-602.

Thomas, D. C. and D. R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada, in COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 1-98 pp.

Thomas, D. C., E. J. Edmonds, and W. K. Brown. 1996. The diet of woodland caribou populations in west-central Alberta. Rangifer, Special Issue **9**:337-342.

Thomas, D. C. 1994. Fire – caribou relationships: (V) The winter diet of the Beverly Herd in northern Canada. Canadian Wildlife Service, Edmonton, Alberta. 41 p.

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management **54**:322-330.

Tracz, B. V. 2005. Woodland caribou (*Rangifer tarandus caribou*) home range and habitat-use relationships to industrial activity in northeastern Alberta. MSc Thesis, University of Alberta, Edmonton, Alberta, Canada.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics **20**:171-197.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893-901.

Walters, C. 1986. Adaptive management of renewable resources. Macmillian Publishing Company. New York, New York, USA.

Chapter 3. Multi-Scale Habitat Selection by Mountain Caribou During the Spring Migratory Period*

1. Introduction

Woodland caribou (*Rangifer tarandus caribou*) populations are declining in west-central Alberta, and the species is classified as threatened in both Alberta and British Columbia, and is listed federally as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Factors recognized as threats to population persistence are habitat alteration and loss, climate change, and predation, although predation is often considered to be a proximate contributor to caribou declines (Thomas & Gray 2002). Caribou have evolved in dynamic landscapes, and can shift their ranges in response to forest succession (Schaefer & Pruitt 1991; Thomas & Gray 2002). However, current rates of landscape change associated with industrial activities are high and extensive (Schneider, 2002) and caribou ranges are being compressed (Smith et al. 2000), reducing options for caribou. In addition to the direct loss of habitat and the displacement from foraging and calving areas (Nellemann & Cameron 1998) as a result of industrial activity, indirect threats due to increased predation risk from increased predator (wolf) access to caribou habitat (James & Stuart-Smith 2000) and the disruption of antipredator strategies, exist (Bergerud & Elliot 1986; Bergerud & Page 1987; Edmonds & Smith 1991; Seip 1991; Rettie & Messier 1998; James et al. 2004).

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As industrial pressures on the landscape escalate, concerns regarding the maintenance of functional habitat and impacts on habitat connectivity increase. Habitat connectivity is necessary for caribou persistence on seasonal ranges (Seip 1991; Rettie & Messier 1998), and at a larger scale for travel between summer and winter ranges. Migration can be defined in a number of ways; I adopted the operational definition of Berger (2004), which considers migration to be a "seasonal round-trip movement between discrete areas not used at other times of the year." Caribou migration is typically associated with the barren ground subspecies (*Rangifer tarandus groenlandicus*), whose bi-annual migrations range between 800 and 5055 kilometers (Fancy et al. 1988; Furguson & Messier 2000). However, some woodland caribou herds also migrate, albeit over less extensive distances (56-300 kilometers; Fuller & Keith 1981; Cumming & Beange 1987; Edmonds 1988). For both subspecies, migration may serve as an effective predator avoidance strategy, with caribou (prey) distancing themselves from predators (primarily wolves) whose movements are restricted during the denning period (Fryxell & Sinclair 1988; Bergerud 1988).

Current industrial activities on caribou ranges are limited to low elevation areas, potentially affecting caribou only during migration and while on the winter range. As a result, considerable attention has focused on aspects of habitat use during the winter months. While the maintenance of winter range is clearly important, I also recognize the need to maintain connectivity between seasonal ranges, as woodland caribou display high fidelity to both summer and winter ranges (Schaefer et al. 2000).

Although the general characteristics of many migratory routes have been documented, little is known about caribou habitat use along these routes, or whether woodland caribou exhibit migration strategies similar to those of migratory avian species, utilizing stopover areas to rest and refuel before resuming their journey (Warnock et al. 2004; LaMontagne et al. 2003; Hedenstrom 2003). I address this by assessing habitat use along migration routes for the Narraway caribou herd in west-central Alberta and east-central British Columbia. The Narraway is unique among caribou ranges in the region, as it has experienced only minor amounts of industrial development. This characteristic allowed me to model habitat selection during migration without the influence of anthropogenic disturbance. The specific objectives of this project were to: 1) quantify the movement patterns of caribou in the Narraway range during the spring migratory period, 2) determine whether these patterns were associated with selection of particular habitat attributes, and 3) investigate the potential mechanisms driving the selection of these habitat attributes. I developed habitat-based, behaviour driven models identifying important coarse-scale attributes of the spring migration routes for the Narraway caribou herd. In addition, I assessed whether the fine-scale attributes associated with use sites were consistent with current migration theory in the context of use of stopover areas for refuelling. I validated coarse-scale models using independent data from additional Narraway caribou.

2. Study Area

My efforts focused on woodland caribou using the Narraway range (approximately 5,000 km^2; Figure 1), located approximately 130 km southwest of Grande Prairie, Alberta, Canada, and extending across the Alberta – British Columbia provincial boundary. In British Columbia, this range is referred to as the Belcourt range. From a regional perspective, this range is unique in that at the time of this study, it existed in a relatively pristine state. Most animals winter (approximately December 1 – April 30) on a large plateau that spans the Alberta - British Columbia border, west of the Narraway River. Much of this area is poorly drained and dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Within this central muskeg area are small patches of upland forest dominated by lodgepole pine (*Pinus contorta*) and black spruce. The winter range is under increasing development pressure from forestry and energy sectors. In the summer (approximately June 15 – October 15), the caribou are found southwest of their winter range in the mountains of British Columbia, near the headwaters of the Narraway and Fraser Rivers. While the summer range is not contained within a protected area, its alpine location currently discourages industrial development. Elevation ranges between 661 m and 3049 m above sea level across the annual Narraway caribou range.

3. Methods

3.1. Caribou Location Data

The 14 adult female caribou used in this study were captured using helicopter-based net gunning techniques. All capture and handling methods were approved by the

University of Alberta, Faculty of Agriculture, Forestry and Home Economics Animal Care Committee (Protocol 2003-29D) and adhered to guidelines outlined by the Canadian Council on Animal Care. Caribou were outfitted with global positioning system (GPS) collars (Lotek GPS 1000 or Lotek GPS 2200, Lotek Engineering, Inc., Newmarket, Ontario, Canada.). Collars were programmed to acquire a fix on one of two schedules: a standard two-hour schedule, or a variable schedule in which locations were acquired every 30 minutes, 2 hours, or 6 hours, depending on the day of the week. While I acknowledge the existence of autocorrelation within the data set, I was interested in selection patterns occurring throughout the entire process of migration and therefore chose not to rarify the data. Use of case-control logistic regression (see Selection Analysis) reduced the effect of autocorrelation on resultant relationships. All locations with HDOP (horizontal dilution of precision) values greater than 12, indicating poor location accuracy, were removed prior to analysis. Models were developed using the migration patterns of 8 caribou across two years (2002-2003; 4 different caribou each year). Data were pooled across years and individuals. For two caribou, I had data for multiple spring migration events. Because caribou tended to use the same route in all years, only the first event for which I had data was used in the analysis. All caribou moved independently of one another in time (i.e. did not migrate together). Data from an additional 6 caribou were used for model validation.

I defined the start of migration on an individual basis, as three consecutive movements of an animal in a SW direction outside the winter range (100% Minimum Convex Polygon for December 1 – April 30 locations). The last cluster of locations

acquired prior to June 15 in any migration event was assumed to represent calving and was removed from the analysis.

3.2. Identification of Scales of Movement

Visual inspection of migration pathways indicated that caribou display punctuated movement during migration, whereby a pattern of traveling followed by a period of limited movement was repeated. To model what was visually apparent in the data, I used a nonlinear curve fitting procedure to identify scales of movement by individual caribou (Sibly et al. 1990; Johnson et al. 2002a; Johnson et al. 2002b). Nonlinear modelling was carried out in SPSS 11.5 (SPSS, Inc). This method approximates a traditional broken-stick model, allowing behaviours to be objectively split into bouts (Sibly et al. 1990). Resting/foraging episodes were assumed to be associated with lower movement rates relative to traveling movements. The nonlinear model takes the form:

$$y = \log_e\left(N_s\lambda_s e^{-\lambda_s r} + N_l\lambda_l e^{-\lambda_l r}\right) \qquad [1]$$

where *s* and *l* refer to processes that are assumed to generate small (resting/foraging) and large scale (traveling) movements; y is the predicted number of movements that occur during each discrete interval of movement rates. N is the number of small and large scale movements that occur at each rate interval, r is the movement rate and λ represents the probability that an event, either resting/foraging or traveling, occurs in the next movement rate interval.

Following model fit, I used the estimated parameters (N, λ) to identify a scale criterion interval (r_c) that defines the break point between large and small-scale movements (Johnson et al. 2002a) and is calculated as follows:

$$r_c = (1/\lambda_s - \lambda_l) * \log_e(N_s \lambda_s / N_l \lambda_l) \qquad [2]$$

Movement rates of caribou less than r_c were considered to be associated with resting/foraging and those greater than r_c were assumed to be associated with traveling.

Resting/foraging locations were often clustered and therefore a lack of independence between successive resting/foraging locations existed. For purposes of evaluating habitat selection, sample size was determined by the number of patches, with patches defined as consecutive locations identified by the nonlinear modelling procedure to be small-scale movements (i.e. clusters of locations classified as resting/foraging). To capture the variation within a patch, I randomly selected three caribou locations, separated by a minimum distance of 100 m, within the patch for analysis. All identified resting/foraging patches and traveling locations were used in the coarse-scale analysis. If the last large-scale movement prior to the caribou entering a defined patch was a distance of less than the location interval multiplied by the scale criterion interval for that caribou, it was reclassified to a resting/foraging location. This reduced the risk of

misclassification, as locations were classified as either small or large-scale movements based on the previous location.

3.3. Habitat Attributes

3.3.1 Coarse-Scale

Habitat attributes used in the modelling procedure were obtained from available forest cover and other spatial data (Table 3.1), within a Geographic Information System (GIS). A grid size of 30 m was used for all environmental and forest cover data, accounting for the error associated with GPS collar locations (D'eon et al. 2002). These data included distance, terrain, and habitat information. Slope, aspect and distances were calculated in the Spatial Analyst extension in ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, CA, USA). I used a terrain ruggedness index (TRI) modified from Nellemann and Fry (1995) to account for local topographic variation. This was calculated using a 300-m circular moving window and the formula:

$$TRI = \frac{(\text{Aspect Variation} * \text{Mean Slope}) / (\text{Aspect Variation} + \text{Mean Slope})}{100}, \quad [3]$$

where aspect variation was the proportion of total number of aspect classes in the moving window over the maximum number of aspect classes within the available landscape (Tuner 1989).

When calculating distance to edge, I defined an edge as any polygon classified as non-forest (e.g., anthropogenic features, lakes, alpine habitat). If a polygon was classified as forest but had a stand density less than 10%; a stand age

of less than 30 years, or had a deciduous component of greater than 70% it was also classed as an edge. I assumed that these forest classes would be recognized as different from the surrounding matrix by caribou.

3.3.2. Fine-Scale

A total of 54 use sites (27 travel and 27 resting/foraging) from the spring 2003 migratory period were sampled in June and August 2003, representing the use of four radio-collared caribou. These sites do not represent a random sample, rather I sampled all identified traveling locations and resting/foraging areas that were accessible. All sites were remote, with no road or trail access. I centered a 30 X 30 m plot at each of the use sites and measured local vegetation characteristics within that area (Table 3.2). Plot dimensions accounted for GPS collar error, which has been estimated at between 5 and 30 m (D'eon et al. 2002). Variables measured at the plot level included canopy cover, slope, aspect and elevation. Within each plot, I randomly placed 6-1 m^2 quadrats. Measurements at this scale focused on evaluating potential caribou forage. I estimated percent vegetation cover for the following categories: terrestrial lichen, moss, forbs, shrubs < or > 10 cm in height, coarse woody debris, bare ground, litter, tree bole, and suspended woody debris. Where possible, I identified all vegetation to the species level and terrestrial lichens were identified as *Cladina mitis, Cladina rangiferina, Cladina spp., Cetraria spp., Cladonia spp., Peltigera spp., Stereocaulon spp.,* and other lichen. Ground layer components (total lichen species, moss, forbs, shrubs < 10 cm, coarse woody debris, bare ground, litter, and tree bole) summed to100%.

In association with each of the quadrats, I estimated the arboreal lichen load below 2.5 m on the tree closest to the center of the quadrat, using broad ordinal classes (Armleder et al. 1992). These classes range from 0-5, with 0 indicating no arboreal lichen present. A height of 2.5 m reflects what would reasonably be accessible as forage for caribou, given a maximum snow depth of about one meter in the study area (Edmonds 1988).

I took the mean value for each attribute sampled at the quadrat level as a representative measure of the plot.

3.4. Modelling Caribou Migration

I conducted a preliminary logistic regression analysis to determine if coarse-scale habitat characteristics differed between resting/foraging sites and traveling sites, and to assess whether modelling the behaviours independently was warranted. All models were estimated using STATA 8.2 (Stata Corporation).

3.4.1. Coarse-Scale Resource Selection

To adequately describe the detected differences between resting/foraging and traveling sites at the coarse scale, I chose to model each behaviour separately. I used case-control logistic regression (Compton et al. 2002) to estimate the logistic discriminant differentiating caribou use sites (either traveling or resting/foraging) from associated randomly generated available locations. This logistic discriminant has been shown to be accurate in differentiating use from available locations (Manly et al. 2002) and is equivalent to an RSF of the form

$\exp(\beta_1 x_1 + \ldots + \beta_p x_p)$ (Manly et al. 2002; Keating & Cherry 2004). Model structure followed the form:

$$w(x) = \exp(\beta_1 x_{ij1} + \beta_2 x_{ij2} + \ldots \beta_K x_{ijK}) \quad [4]$$

where $w(x)$ is the relative probability of use for the jth resource unit being selected at the ith choice for the predictor variables, x_i, and the β_i's are the coefficient estimates for each predictor variable.

Fourteen candidate models were developed *a priori*, based on biologically relevant habitat attributes (Table 3.3). All predictor variables were examined for collinearity using Pearson correlations. Collinearity between individual parameters was assumed if correlations were > |0.7|. Correlated variables that consistently explained the most deviance from the null model were retained. I tested all models for multicollinearity (Menard 1995) using variance inflation factors (VIF). Multicollinearity was a concern if individual parameter VIF values were > 10 or if the mean VIF score for a given model was considerably larger than 1 (Chatterjee et al. 2000). If models exhibited multicollinearity they were removed from the candidate set. Model selection was based on AIC_c (Akaike's Information Criteria, corrected for small sample size bias; Anderson & Burnham 2002), which balances model fit with model parsimony. Models were ranked based on the difference in the AIC_c values (ΔAIC_c), and Akaike weights (w_i) were used to assess the strength of evidence that any particular model was the best model in my set of candidate models (Anderson et al. 2000). I assessed the effect of individual parameters in the AIC-selected model using 95% confidence

intervals; coefficients whose confidence intervals did not overlap zero contributed to the model. The ability of the models to accurately predict resting/foraging or traveling was determined through the validation process.

3.4.2. Coarse-Scale Selection Analysis

I used case-control logistic regression to account for the spatial and temporal variation in habitats (Pendergast et al. 1996), by defining availability based on each travel location or resting/foraging patch. Following Arthur et al. (1996), random locations were generated within a circle centered on the preceding use location with a radius either equal to the 95th percentile of the distance traveled for that location interval (30 min, 1 hr, 2 hr, 4 hr, 6 hr, 10 hr, 12 hr, and 18 hr) averaged across all animals or the distance between the two locations, which ever was larger. For locations identified as traveling by the non-linear modelling procedure, 20 random points were generated to represent available locations. Locations identified as resting/foraging required the following additional steps to replicate the clustered nature of the use locations. Twenty random points were generated as per traveling locations. Each point was then buffered by the average area of all resting/foraging use patches (276 meter radius). Within this buffer area, 3 random points were generated to compare against the 3 known use locations.

The locations of all random points, and hence available habitat, was limited to elevations less than 2,000 meters and habitat classed as either a lake or river was excluded. Consistent with selection of use points within

resting/foraging areas, random points were a minimum of 100 meters apart. Random point generation was carried out using Hawth's Analysis Tools extension (Version 2.0) in ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, CA, USA).

3.4.3. Fine-Scale Resource Selection

I evaluated the selection of fine-scale habitat attributes at resting/foraging locations relative to traveling locations using logistic regression. Resting/traveling locations identified through the non-linear modelling procedure were classified as 1's and traveling locations as 0's.

This data structure allowed us to develop resource selection probability functions (RSPF; Manly et al. 2002) and model structure followed the form:

$$w^*(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots \beta_i x_i)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots \beta_i x_i)} \qquad [5]$$

where $w^*(x)$ is the resource selection probability function, β_0 is a constant, β_i is the selection coefficient for the x_i^{th} covariate.

I used the Huber-White sandwich variance estimator (Pendergast et al. 1996) as a variance inflator. This method does not affect coefficient estimates, but allows robust standard errors to be calculated, accounting for lack of independence between individual observations (Pendergast et al. 1996). This was necessary due to the clustered nature of resting/foraging locations.

Variables were examined for collinearity as previously described. I further reduced the number of variables included in the model building process by running univariate logistic regressions on all remaining covariates (Zielinski et al. 2004). Those with relatively important β values ($P < 0.25$ threshold; Hosmer & Lemeshow 2000) were retained as potentially important in distinguishing resting/foraging and traveling sites. The remaining variables (Table 3.2) were used to construct 21 candidate models (Table 3.4). I assessed model fit using the Wald chi square statistic (Hosmer & Lemeshow 2000). I tested all models for multicollinearity, and model selection and evaluation proceeded as per the coarse-scale process.

3.5. Spatial Interpolation

The best model for each behaviour was incorporated into a GIS framework (ArcGIS 8.3; Environmental Systems Research Institute, Redlands, CA, USA), and used to produce maps depicting a relative index of use for traveling or resting/foraging. Maps were area-adjusted, and relative index of use was assigned to 10 quantile bins, containing equal proportions.

3.6. Model Validation

3.6.1. Coarse-Scale

As my study design at this scale was based on used and available locations, model validation through Receiver Operating Characteristic (ROC) curves was inappropriate (Boyce et al. 2002). However, I was able to use

independent location data from an additional six caribou for model validation. I classified each of these locations as either traveling or resting/foraging using the same non-linear modelling procedures used for classification of the locations used in model building. The behaviour-specific relative index maps, derived from the AIC-selected models, were then evaluated for their ability to predict use through a Spearman rank correlation, $\alpha = 0.05$. Independent data points classified as traveling were used to assess the travel index surface, while those classified as resting/foraging were used to assess the index surface for resting/foraging. Strong correlations of the predicted map bins with independent validation data were taken to indicate good model fit and prediction. I use the term "index", rather than "probability" when referring to relative use, in response to recent criticisms from Keating and Cherry (2004) regarding estimation of relative probability surfaces from use-availability designs. However, I note that their concerns were particularly acute in situations where higher order polynomials were being modelled, and my most complex models include only a quadratic term.

3.6.2. Fine-Scale

The study design at this scale allowed the use of ROC curves (Swets 1988) to validate fine-scale models and assess model fit. Model performance based on ROC scores can be grouped into three categories. Values ranging between 0.5 and 0.7 are considered to have low model accuracy; those between 0.7 and 0.9 are thought to have good model accuracy, while those above 0.9 indicate high model accuracy (Swets 1988).

4. Results

4.1. Caribou Relocations

The eight caribou used for model building followed one of two main routes (Figure 2). While the general route traveled may be the same for multiple caribou, no radio-collared caribou were traveling together during the migratory period. Therefore the decision to rest/forage or continue traveling was independent of the presence of other radio-collared caribou. Two caribou migrated through the northern part of the range using the Red Deer Creek area. A third animal used this area in 2003 but died early in migration and was excluded from the analysis. The remaining six caribou used the Narraway River region (Figure 2; Table 3.5). Route selection varied more in this area than in the northern region, with some caribou traversing Ptarmigan Mountain before entering the Narraway Valley, while others went around. Variation was also apparent in the extent of travel in the Narraway River valley. Some caribou remained in this valley until they reached their calving grounds, while others branched off, using the Belcourt Creek drainage (Figure 2; Table 3.5). The departure dates from the winter range, overall distance traveled, and duration of migration also varied among caribou and year (Table 3.5).

4.2. Identification of Scales of Movement

Non-linear modelling identified the movement rate above which locations were classified as traveling and below which they were classified as resting/foraging (Table 3.6). The rate at which behaviours were differentiated

was variable among individuals and migration strategies also appeared to vary among caribou with some traveling quickly and spending more time at resting/foraging areas and while others traveled at a slower rate and spent less time in resting foraging areas. The migration strategy used and the collar schedule influenced the number of locations each animal contributed to the data set, such that the locations were not balanced across animals. Regardless of the strategy used, I assumed that caribou used similar habitats for each of the behaviours.

Of the 176 caribou locations available for model building, 78 were identified as resting/foraging and 98 as traveling locations. The 78 resting/foraging locations represented 28 patches, thus the sample size for statistical analysis was 28 for resting/foraging models and 98 for traveling models (Table 3.7).

4.3. Modelling Caribou Migration

Discrimination was possible between habitats associated with resting/foraging and traveling sites, providing justification for modelling the behaviours separately. Resting/foraging locations were further from water and in less dense, older forests than were traveling locations.

4.3.1. Coarse-Scale Traveling

Of 14 candidate RSF models (Table 3.3), Model M3-13 was identified as the best model. This model indicated that travel locations were more likely to be

associated with less rugged terrain and were closer to water than random available locations. The model takes the form:

$$\hat{w} = -8.921(TRI) - 0.375(distwater) \quad [6]$$

The confidence intervals for TRI did not overlap zero, indicating that this variable had a strong influence on selection. The low Akiake weight associated with this model (0.423; Table 3.8), suggests only weak support that this model is the best predictive model. However, the second ranked model (Model M3-12) was also a 2-term model, and contained the TRI covariate, whose coefficient is consistent over both models. In addition, the second variable in Model M3-12, distedge, is a composite variable containing distwater, although it is not correlated with it. I was thus confident in selecting Model 13 as the top AIC model and incorporated it into a GIS framework identifying suitable traveling habitat for caribou (Figure 3a). There was a significant positive correlation between the travel index surface and the occurrence of travel locations from the independent data set ($r_{(s)} = 0.636$, $P = 0.048$). I interpreted this as evidence that the model was reasonably robust.

4.3.2. Coarse-Scale Resting/Foraging

Similarly, of the 14 candidate models evaluated for resting/foraging locations (Table 3.3), Model M3-14 was identified as the best model, indicating that resting/foraging locations were more likely to be associated with older forests that have a greater component of pine, and were further from water than were random available locations. The model takes the form:

$$\hat{w} = 0.015(age) - 0.00003(age^2) + 0.008(pine) + 1.181(distwater) \quad [7]$$

The confidence intervals for age, pine, and distwater did not overlap zero, suggesting they had a strong influence on habitat selection. The Akiake weight associated with this model was 0.633, indicating a moderate level of confidence that this model was the best of those considered, given the data (Table 3.9). I used this model to generate a predictive map indicating the occurrence of potential resting/foraging habitat for caribou during the spring migration (Figure 3b). There was a significant positive correlation between the resting/foraging index surface and the occurrence of resting/foraging locations from the independent data set ($r_{(s)} = 0.697$, $P = 0.025$), indicating that this model was reasonably robust.

4.3.3. Fine-Scale

Of the 32 variables measured at the plot level, nine were retained for use in the model building process (Table 3.2). Twenty-one candidate models were evaluated and M4-21 was identified as the best model (Table 3.10). While the model fit was not significant (Wald $\chi^2_{(5)} = 10.15$; $P = 0.071$), it explained approximately 34% of the observed variation. Poor model fit is likely a result of the limited sample size. This model suggested that, at the 30 m plot level, caribou resting/foraging locations were associated with more arboreal lichen, a greater component of white spruce, a more open canopy, less litter but more shrubs > 10 cm in height when compared to traveling locations. The model took the form,

$$\hat{w} = 0.283 + 2.121(Arb_Cat) + 0.019(Shrub > 10cm) - 0.065(Litter) + 0.043(\%SW) - 0.065(Canopy). \quad [8]$$

The confidence intervals for Arb_Cat, Litter, and % SW did not overlap zero, suggesting they had a strong influence on habitat selection. The Akiake weight associated with this model was 0.574, indicating a low level of confidence that this model was the best of those considered, given the data (Table 3.10). The ROC score associated with this model was 0.855, indicating good model accuracy.

5. Discussion

In west central Alberta, all caribou winter ranges fall under Forest Management Agreements, and are subject to timber harvest as well as increasing pressures from the oil and gas sectors. The identification of specific habitat attributes associated with caribou use is critical to the successful integration of caribou conservation strategies and sustainable land use management practices. Most attention has focused on the reduction of industrial effects on caribou winter ranges because these are thought to be most limiting (Bjorge 1984; Thomas et al. 1996) and subject to the greatest development pressure (Hervieux et al. 1996). However, as industrial activity expands, effects are reaching beyond the winter ranges and potentially influencing the use of traditional migration routes, and therefore affecting connectivity between summer and winter ranges.

This study is the first attempt I am aware of to link observed movement patterns to habitat selection by woodland caribou during migratory events. I

demonstrated that mountain caribou selected certain habitat characteristics during migration and that this selection depends on movement behaviour, as inferred by the rate at which they are moving. When traveling, caribou selected habitat that was closer to water and in less rugged terrain than random locations. This is consistent with least resistance theory (Hedenstrom 2003), which hypothesizes animals will choose to travel in areas where they are able to move more quickly and expend less energy, typical of animals traveling between stopover sites. In a mountainous environment, these conditions are met along major drainages. When resting or foraging, caribou moved away from water bodies and into 'old' pine stands. These habitats are also consistent with migration theory, which suggests that stopover areas are used for refuelling, resting and shelter (Hedenstrom 2003) and occur in areas with relatively less predation risk (Berthold & Terrill 1991). Although this scale does not address potential mechanisms, the habitat attributes associated with these areas are consistent with those of higher forage (terrestrial lichen and forb) abundance (Pharo & Vitt 2000). I associate risk of predation with distance to water, as wolves are known to travel along natural (Huggard 1993) and anthropogenic (James 1999) features at increased rates, thus increasing the likelihood of a predator-prey encounter (James 1999; Dzus 2001).

Investigation of the fine-scale habitat attributes differentiating resting/foraging locations from traveling locations also supports the hypothesis that these areas are used for refueling along the migration route, although arboreal lichen abundance was shown to be more influential than terrestrial lichen.

However, this result should be interpreted cautiously as sample size was limited for this analysis.

One of the primary hypotheses for migration by mountain caribou is separation from predators during the vulnerable calving period (Edmonds 1988; Seip 1991; Edmonds & Smith 1991). Increased habitat alteration and fragmentation associated with development on migratory routes connecting caribou summer and winter ranges could have two main effects. First, changes in predator abundance and distribution are likely (Dzus 2001). As mature forests are replaced with younger forests post harvest, an increase in the abundance of other ungulate species is expected, which in turn will support larger populations of predator species (Rettie & Messier 1998; Kunkel & Pletscher 2000; James & Stuart-Smith 2000). Predator distribution may also be enhanced as they may gain access to previously remote areas through travel on anthropogenic linear features (Dzus 2001), leading to increased encounter rates with, and mortality rates for, caribou (Seip 1992; James 1999; James & Stuart-Smith 2000; James et al. 2004). Secondly, increased habitat alteration and fragmentation associated with industrial activity may lead to increased energetic costs, if caribou attempt to avoid these developments (Nellemann & Cameron 1998; Vistnes & Nellemann 2001; Dyer et al. 2001). Migration is characteristically a balance between energetic outputs for locomotion and energetic inputs in the form of fuel intake (Hedenstrom 2003). Detours are only possible when alternate areas for foraging exist and can be located without upsetting this balance (Alerstam 2001; Hedenstrom 2003). This has implications for long-term caribou persistence, as cows may arrive in the

alpine in poor condition, effecting both the survival of the cow and her offspring. Ultimately, the cumulative effect of incremental development may result in the abandonment of migration routes all together (Alerstam et al. 2003). If caribou cease migrating, they may be exposed to higher predation risk year-round if they stay on winter ranges, or experience reduced condition if they remain in less productive alpine summer ranges.

The limited number of caribou included in this study necessitated pooling data across years and individuals. I acknowledge that by pooling I may have masked individual variation in selection of habitats by caribou or variation due to changing environmental conditions across years. However, management cannot take place at the level of the individual or even on a yearly basis, in most cases. Global models may thus be most appropriate for management purposes, provided they have been validated. Independent validation of the models is particularly important when, as in this case, the sampling design is unbalanced. Animals that are more prevalent in the data set, will contribute more information to the models, having a greater influence on the resulting selection coefficients. As my models adequately predicted the occurrence of independent caribou locations on the landscape I do not believe that any one animal from the model building set had undo influence on my models, and that my assumption that habitat selection was consistent across years and individuals was appropriate, at least within the confines of this study. Where sample sizes permit, individual models should be built to substantiate this assumption prior to pooling of data. Data collection over a greater number of years would better represent longer-term environmental variation, and resultant implications for habitat selection.

Migration is an important, and often neglected, component of the life history of mountain caribou, and should be accounted for in conservation planning. The models produced here, while specific to the Narraway range in west central Alberta, represent an important link between migratory behaviour and habitat use. As a visual representation of these models, the maps allow for the identification of habitats selected during migration. These maps provide guidance for land-use planners when evaluating management options.

Table 3.1: GIS predictor variables used to model coarse-scale habitat selection along the spring migratory pathways of woodland caribou using the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada (2002-2003). All response variables were continuous.

Variable Code	Name	GIS Data Source
elev	Elevation (m)	Digital Elevation Model (DEM)[c]
TRI	Terrain Ruggedness Index	DEM spatial analyst calculation
Distwater[a]	Distance to Water (km)	Spatial Analyst calculation
Distedge[b]	Distance to Edge (km)	Spatial Analyst calculation
age	Stand Age (yr)	Forest cover layer[d]
age^2	Stand Age Quadratic (yr^2)	Calculated from forest cover layer
density	Canopy Cover (%)	Forest cover layer
spruce	% Spruce	Forest cover layer
pine	% Pine	Forest cover layer

[a] Distance to closest permanent water source.
[b] Distance to closest natural or anthropogenic edge. Natural edges included any non-forest classed polygon and forest polygons whose density was < 10%, or whose age < 30 years, or that had a deciduous component of > 70%.
[c] The DEM was obtained from the National Topographic Data Base.
[d] Forest cover layers were provided by Weyerhaeuser Company (Alberta) and the British Columbia Ministry of Forests.

Table 3.2: Variables considered for the comparison of fine-scale habitat attributes selected at resting/foraging sites *vs.* traveling sites during the 2003 spring migratory period for caribou using the Narraway range in west-central Alberta and east-central British Columbia, Canada.

Variables	Description	*P*
ALC	Average arboreal lichen class	0.209*
% *Cladina mitis*	Average % cover of *C. mitis*	0.182*
% *Cladina rangiferina*	Average % cover of *C. rangiferina*	0.355
% *Cladina spp*	Average % cover of *Cladina spp*	0.440
% *Cladonia spp*	Average % cover of *Cladonia spp*	0.864
% *Cetraria spp*	Average % cover of *Cetraria spp*	0.595
% *Stereocaulon spp*	Average % cover of *Stereocaulon spp*	0.195*
% *Peltigera spp*	Average % cover of *Peltigera spp*	0.387
% Other Lichen Species	Average % cover of other lichen species	0.216†
% Total Lichen species	Average total lichen % cover over	0.470
% Moss	Average % cover of moss	0.515
% Forbs	Average % cover of forbs	0.876
% Grass	Average % cover of grass	0.817
% Sedge	Average % cover of sedge	0.611
% Shrubs < 10 cm	Average % cover of shrubs < 10 cm in height	0.286
% Litter	Average % cover of litter	0.085
% CWD	Average % cover of coarse woody debris	0.754
% Bare Ground	Average % bare ground within the plot	0.666
% Tree Bole	Average % ground cover occupied by tree boles	0.769
% Shrubs > 10 cm	Average % cover of shrubs > 10 cm in height	0.104*
% SCW	Average % cover of suspended coarse woody debris	0.796
% PL	Proportion of trees that were pine	0.207*
% SB	Proportion of trees that were black spruce	0.554
% SW	Proportion of trees that were white spruce	0.035*
% FR	Proportion of trees that were fir	0.222*
Canopy	Estimated canopy cover over the 30m plot	0.117*
Slope	Predominant slope over the 30m plot	0.567
Aspect	Predominant aspect over the 30m plot	0.950
Elevation	Elevation at the centre of the 30m plot	0.881

* For variable reduction purposes, univariate case-controlled logistic regressions were carried out. Variables with $P \leq 0.25$ (*) were retained for use in fine-scale caribou occurrence model building.

† Variable not used in model building due to low number of records.

Table 3.3: *A priori* candidate models used in assessing coarse-scale habitat selection for traveling and resting/foraging during the spring migratory period on the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada. Models were parameterized using caribou location data from the 2002 and 2003 spring migratory periods.

Model #	Model
M3-1	Age + age^2 + distwater + distedge + pine + TRI
M3-2	Distwater + age + age^2
M3-3	Distwater
M3-4	Pine + age + age^2
M3-5	Spruce + age + age^2
M3-6	TRI + age + age^2
M3-7	Age + age^2
M3-8	Pine + density
M3-9	Spruce + density
M3-10	Pine + distwater + density
M3-11	TRI + density
M3-12	TRI + distedge
M3-13	TRI + distwater
M3-14	Pine + distwater + age + age^2

Table 3.4: *A priori* candidate models used in assessing fine-scale habitat attributes associated with Narraway caribou in west-central Alberta and east-central British Columbia, Canada resting/foraging locations during the 2003 spring migratory period.

Model #	Model Structure
FORAGE MODELS	
M4-1	ALC
M4-2	ALC + % C. *mitis*
M4-3	ALC + % C. *mitis* + % *Stereocaulon spp*
M4-4	% *C. mitis*
M4-5	% C. *mitis* + % *Stereocaulon spp*
GROUND STRUCTURE MODELS	
M4-6	% Shrubs > 10 cm
M4-7	% Litter
M4-8	% Shrubs > 10 cm + % Litter
FOREST STUCTURE MODELS	
M4-9	% FR
M4-10	% PL
M4-11	% SW
M4-12	Canopy
M4-13	% PL + % FR + % SW
M4-14	% PL + Canopy
M4-15	% FR + Canopy
M4-16	% SW + Canopy
M4-17	% PL + % FR + % SW + Canopy
COMBINATION MODELS	
M4-18	Model M4-1+ Model M4-8
M4-19	Model M4-1 + Model M4-16
M4-20	Model M4-8 + Model M4-16
M4-21	Model M4-1 + Model M4-8 + Model M4-16

Table 3.5: General characteristics of the spring migration (2001 – 2002) for collared woodland caribou using the Narraway range in west central Alberta and east-central British Columbia, Canada. The reported migration distance is the cumulative distance between the first identified migration location and the estimated calving location.

Model Building					
Year	Caribou ID	Path	Migration Distance (km)	Duration of Migration (hours)	Departure Date
2002	F709	Narraway	25.3	24	05/25/02
2002	F710	Red Deer Creek	27.5	40	05/27/02
2002	F711	Red Deer Creek	32.5	55	05/28/02
2002	F712	Narraway	73.1	300	06/03/02
2003	F715	Narraway via Ptarmigan	29.4	142	05/29/03
2003	F717	Narraway/Belcourt via Ptarmigan	70.1	116	05/22/03
2003	F722	Narraway/Belcourt via Ptarmigan	73.9	238	05/23/03
2003	F723	Narraway via Ptarmigan	119.1	206	05/16/03
		Mean ± SE	**56.4 ± 11.8**	**140 ± 36**	
Model Validation					
Year	Caribou ID	Path	Migration Distance (km)	Duration of Migration (hours)	Departure Date
2001	F702	Narraway	145.2	360	05/11/01
2001	F704	Belcourt	33.2	75	05/06/01
2001	F705	Narraway/Belcourt	102.8	249	05/15/01
2002	F700	Narraway/Belcourt	76.8	246	05/29/02
2002	F708	Narraway via Ptarmigan	141.5	588	05/11/02
2003	F713	Red Deer Creek	64.9	308	05/11/03
		Mean ± SE	**94.1 ± 18.1**	**304 ± 69**	

Table 3.6: The rates (r_c) identified by non-linear modelling below which caribou locations from the Narraway range in west-central Alberta and east-central British Columbia, Canada during the spring migratory period, 2001 – 2003, were classified as resting/foraging and above which they were classed as traveling.

Model Building			**Model Validation**		
Year	Caribou ID	r_c (m/min)	Year	Caribou ID	r_c (m/min)
2002	F709	2.64	2001	F702	6.02
2002	F710	2.99	2001	F704	3.12
2002	F711	3.69	2001	F705	3.71
2002	F712	2.62	2002	F700	4.28
2003	F715	2.61	2002	F708	4.52
2003	F717	5.35	2003	F713	8.94
2003	F722	3.10			
2003	F723	9.81			
	Mean ± SE	**4.10 ± 0.88**		**Mean ± SE**	**5.10 ± 0.87**

Table 3.7: Caribou locations used in coarse-scale analysis of habitat selection along the spring migratory path of the Narraway Caribou Herd, west central Alberta and east-central British Columbia, Canada, 2001 - 2003. Resting/foraging and traveling movements were defined by non-linear modelling procedures.

Model Building					
Year	Caribou ID	# Patches	# Resting/Foraging Locations	# Traveling Locations	# Areas
2002	709	1	1	3	4
	710	2	6	17	19
	711	1	3	9	10
	712	4	11	7	11
Sub Total	**4**	**8**	**21**	**36**	**44**
2003	715	2	6	2	4
	717	4	10	10	14
	722	7	15	21	28
	723	7	21	29	36
Sub Total	**4**	**20**	**52**	**62**	**82**
Total	**8**	**28**	**73**	**98**	**126**
Model Validation					
Year	Caribou ID	# Patches	# Resting/Foraging Locations	# Traveling Locations	# Areas
2001	702	14	30	18	32
	704	4	10	4	8
	705	7	15	19	26
Sub Total	**3**	**25**	**55**	**41**	**66**
2002	700	8	22	6	14
	708	12	31	15	27
Sub Total	**2**	**20**	**53**	**21**	**41**
2003	713	3	9	3	6
Sub Total	**1**	**3**	**9**	**3**	**6**
Total	**6**	**48**	**117**	**65**	**113**

Table 3.8: A comparison of coarse-scale habitat use models characterizing traveling locations of Narraway caribou during the 2002 & 2003 spring migration. Models are ranked by Δ AIC_c values. Akaike weights (w_i) indicate the likelihood of the model being the best of those tested. K indicates the number of parameters in the model.

Model #	K	AIC_c	Δ AIC_c	w_i	Rank
13	2	582.5943	0.000	0.423	1
12	2	583.0963	0.502	0.329	2
11	2	583.8423	1.248	0.227	3
1	6	589.0851	6.491	0.016	4
3	1	593.1357	10.541	0.002	5
2	3	595.3133	12.719	< 0.001	6
14	4	596.6661	14.072	< 0.001	7
10	3	596.8473	14.253	< 0.001	8
7	2	598.3683	15.774	< 0.001	9
4	3	599.5813	16.987	< 0.001	10
8	2	600.2523	17.658	< 0.001	11
9	2	600.3663	17.772	< 0.001	12
5	3	600.4973	17.903	< 0.001	13
6	3	602.7233	20.129	< 0.001	14

Table 3.9: A comparison of coarse-scale habitat use models characterizing resting/foraging locations of Narraway caribou during the 2002 & 2003 spring migration. Models are ranked by Δ AIC_c values. Akaike weights (w_i) indicate the likelihood of the model being the best of those tested. K indicates the number of parameters in the model.

Model #	K	AIC_c	Δ AIC_c	w_i	Rank
14	4	486.673	0.000	0.633	1
2	3	488.000	1.327	0.326	2
1	6	492.194	5.521	0.040	3
4	3	501.284	14.611	<0.001	4
7	2	502.436	15.763	<0.001	5
5	3	503.038	16.365	<0.001	6
6	3	504.974	18.301	<0.001	7
13	2	508.356	21.683	<0.001	8
10	3	510.088	23.415	<0.001	9
3	1	516.158	29.485	<0.001	10
12	2	516.766	30.093	<0.001	11
9	2	519.402	32.729	<0.001	12
11	2	519.814	33.141	<0.001	13
8	2	519.954	33.281	<0.001	14

Table 3.10: A comparison of fine-scale habitat models used to characterize locations of resting/foraging caribou during the spring migratory period, 2003. Models are ranked by Δ AICc values. Akaike weights (w_i) indicate the likelihood of the model being the best of those tested. K indicates the number of parameters in the model.

Model #	K	AIC_c	Δ AIC_c	w_i	Model Rank
FORAGE MODELS					
M4-1	2	73.686	0.000	0.396	1
M4-2	3	74.706	1.020	0.238	2
M4-5	3	75.716	2.030	0.143	3
M4-3	4	75.728	2.043	0.142	4
M4-4	2	76.856	3.170	0.081	5
GROUND STRUCTURE MODELS					
M4-8	3	74.012	0.000	0.541	1
M4-6	2	75.500	1.488	0.257	2
M4-7	2	75.990	1.978	0.201	3
FOREST STRUCTURE MODELS					
M4-15	3	71.258	0.000	0.281	1
M4-17	5	71.526	0.268	0.246	2
M4-11	2	72.066	0.808	0.188	3
M4-16	3	72.758	1.500	0.133	4
M4-13	4	74.382	3.124	0.059	5
M4-12	2	75.716	4.458	0.030	6
M4-14	3	76.222	4.964	0.024	7
M4-9	2	76.548	5.290	0.020	8
M4-10	2	76.680	5.422	0.019	9
COMBINATION MODELS					
M4-21	6	64.411	0.000	0.631	1
M4-19	4	66.870	2.460	0.184	2
M4-20	5	67.102	2.691	0.164	3
M4-18	4	71.248	6.838	0.021	4
ALL MODELS					
M4-21	6	64.411	0.000	0.574	1
M4-19	4	66.870	2.460	0.168	2
M4-20	5	67.102	2.691	0.150	3
M4-18	4	71.248	6.838	0.019	4
M4-15	3	71.258	6.847	0.019	5
M4-17	5	71.526	7.115	0.016	6
M4-11	2	72.066	7.655	0.013	7
M4-16	3	72.758	8.347	0.009	8
M4-1	2	73.686	9.275	0.006	9
M4-8	3	74.012	9.601	0.005	10
M4-13	4	74.382	9.972	0.004	11
M4-2	3	74.706	10.295	0.003	12
M4-6	2	75.500	11.089	0.002	13
M4-12	2	75.716	11.305	0.002	14
M4-5	3	75.716	11.305	0.002	15
M4-3	4	75.728	11.318	0.002	16
M4-7	2	75.990	11.579	0.002	17
M4-14	3	76.222	11.811	0.002	18
M4-9	2	76.548	12.137	0.001	19
M4-10	2	76.680	12.269	0.001	20
M4-4	2	76.856	12.445	0.001	21

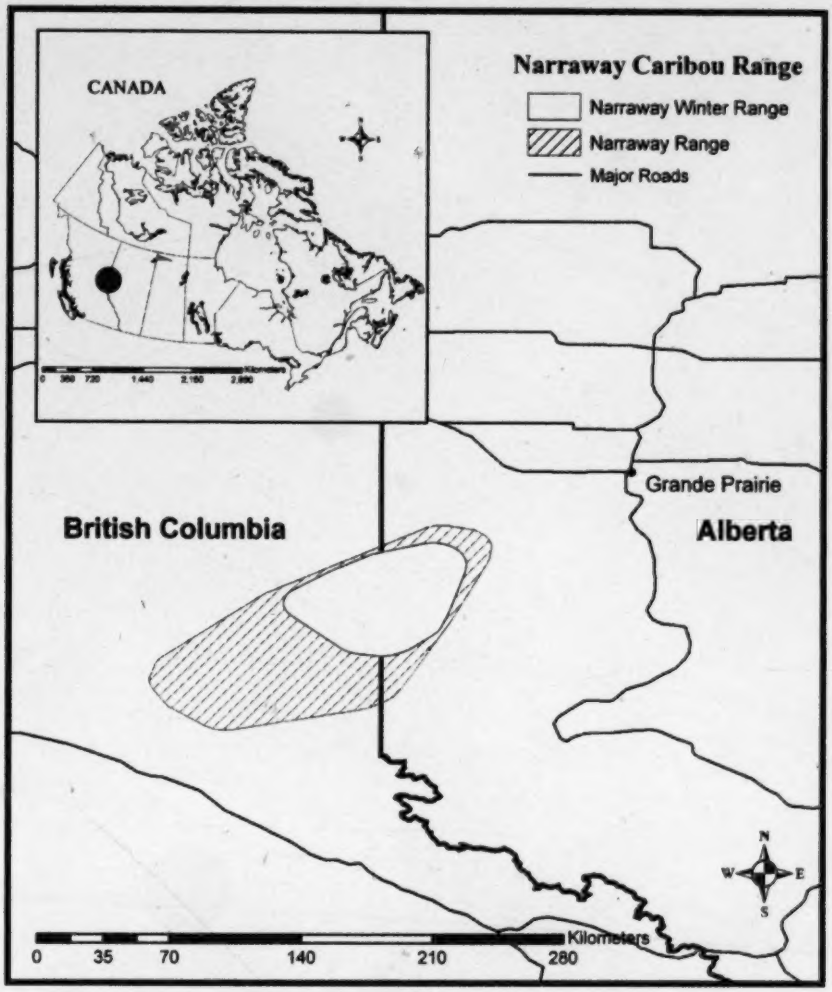

Figure 3.1: The Narraway caribou range, located in west-central Alberta and east-central British Columbia, Canada.

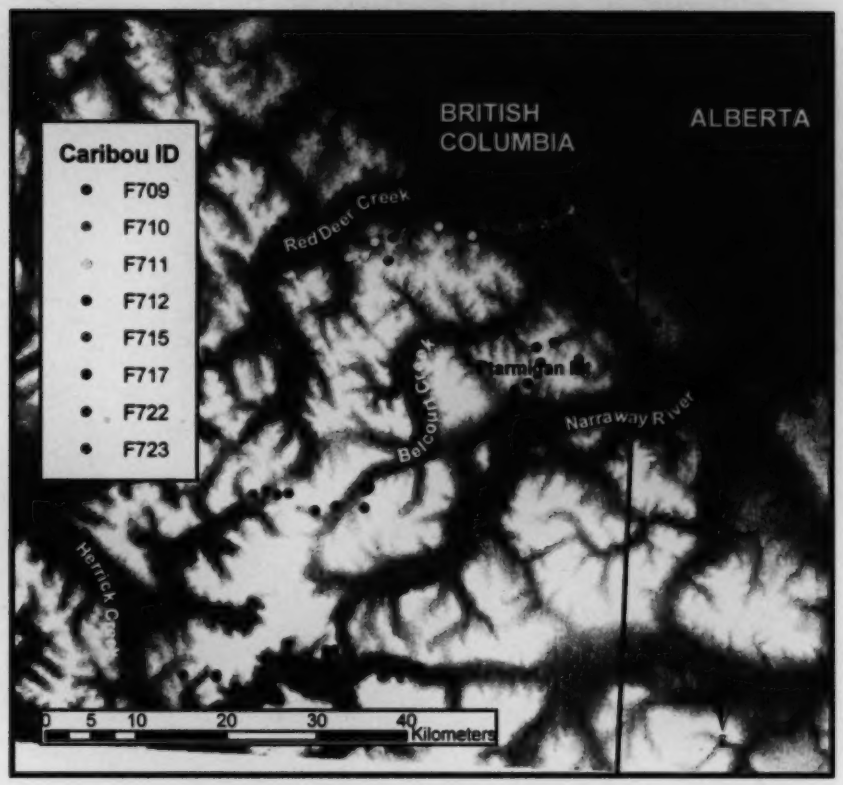

Figure 3.2: General pathways taken during the spring migration (2002 & 2003) of collared Narraway caribou in west-central Alberta and east central British Columbia, Canada.

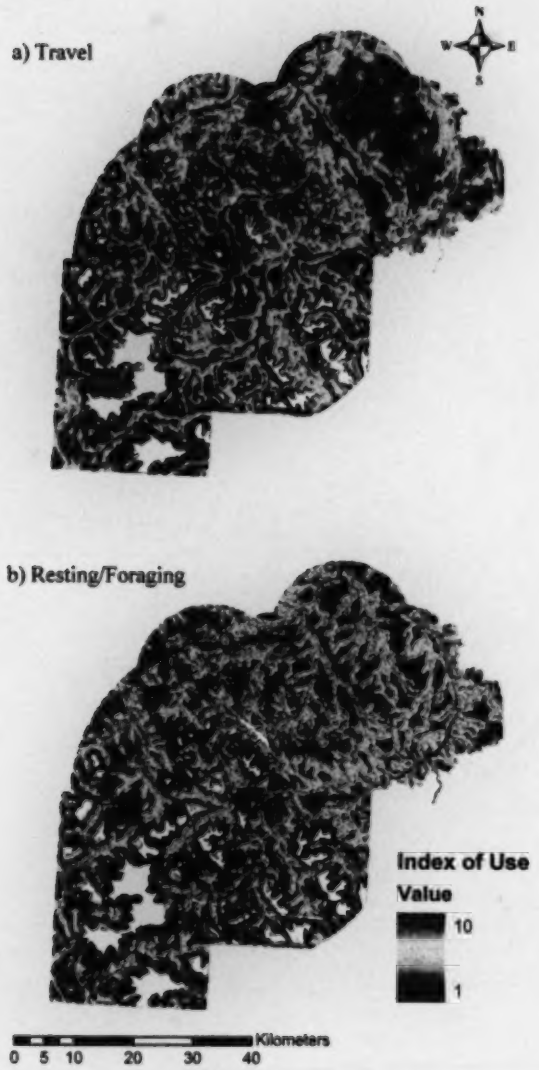

Figure 3.3: Interpolated map surface showing the relative index of use during the spring migration on the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada (2002 & 2003). The relative index of use for traveling is shown in (a) and that for resting/foraging in (b). Warm colors indicate a relatively high index value and cool colors indicate a relatively low index value. White reflects areas that were excluded from sampling either as water bodies or elevations greater than 2000 meters.

6. Literature Cited

Alerstam T. 2001. Detours in bird migration. Journal of Theoretical Biology **209**:319-331.

Alerstam T., A. Hedenstrom, and S. Akesson. 2003. Long-distance migration: evolution and determinants. Oikos **103**:247-260.

Anderson D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management **64**:912-923.

Anderson D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management **66**:912-918.

Armleder H. M., S. K. Stevenson, and S. D. Walker. 1992. Estimating the abundance of arboreal forage lichens. B.C. Ministry of Forests. Victoria, BC.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner 1996. Assessing habitat selection when availability changes. Ecology **77**: 215-227.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology **18**: 320-331.

Bergerud A. T. 1988. Caribou, wolves and man. Trends in Ecology & Evolution **3**:68-72.

Bergerud A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology **64**:1515-1529.

Bergerud A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology **65**:1597-1606.

Berthold P., and S. B. Terrill. 1991. Recent advances in studies of bird migration. Annual Review of Ecology and Systematics **22**:357-378.

Boyce M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281-300.

Chatterjee, S., A. S. Hadi, and B. Price. 2000. Regression analysis by example. 3rd Edition. John Wiley & Sons, Inc. New York, New York, USA.

Compton B. W., J. M. Rhymer, and M. Mccollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology **83**:833-843.

Cumming H. G., and D. B. Beange. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. Journal of Wildlife Management **51**:69-79.

D'eon R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin **30**:430-439.

Dyer S. J., J. P. O'neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management **65**:531-542.

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, Alberta. 47pp.

Edmonds E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. Canadian Journal of Zoology **66**:817-826.

Edmonds, E. J. and K. G. Smith. 1991. Mountain caribou calf production and survival, and calving and summer habitat use in west-central Alberta. Alberta Environment, Fish and Wildlife Division, Wildlife Research Series No. 4. Edmonton, Alberta. 1-16 pp.

Fancy S. G., L. F. Prank, K. R. Whitten, and W. L. Regelin. 1988. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology **67**:168-178.

Fryxell J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution **3**:237-241.

Fuller T. K., and L. B. Keith. 1981. Woodland Caribou Population-Dynamics in Northeastern Alberta. Journal of Wildlife Management **45**:197-213.

Furguson M. A. D., and F. Messier. 2000. Mass emigration of Arctic tundra caribou from traditional wintering range: population dynamics and physical condition. Journal of Wildlife Management **64**:168-178.

Hedenstrom A. 2003. Optimal migration strategies in animals that run: a range equation and its consequences. Animal Behaviour **66**:631-636.

Hervieux D., J. Edmonds, R. Bonar, and J. McCammon. 1996. Successful and unsuccessful attempts to resolve caribou management and timber harvesting issues in west central Alberta. Rangifer, Special Issue **9**:185-190.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. John Wiley & Sons, Inc. New York, New York, USA.

Huggard D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management **52**:382-388.

James A. R. C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. PhD Dissertation. University of Alberta, Edmonton, Alberta.

James A. R. C., S. Boutin, D. M. Herbert, and A. B. Rippen. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management **68**:799-809.

James A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management **64**:154-159.

Johnson C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002a. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology **71**:225-235.

Johnson C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002b. A multiscale behavioural approach to understanding the movements of woodland caribou. Ecological Applications **12**:1840-1860.

Keating K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management **68**:774-789.

Kunkel K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology **78**:150-157.

LaMontagne J. M., L. J. Jackson, and R. M. R. Barclay. 2003. Characteristics of ponds used by trumpeter swans in a spring migration stopover area. Canadian Journal of Zoology **81**:1791-1798.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.

Menard, S. 1995. Applied logistic regression analysis. Sage University Paper Series on Quantitative Applications in the Social Sciences, 07-106. Sage Publications. Thousand Oaks, California, USA.

Nellemann C., and R. D. Cameron. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology **76**:1425-1430.

Nellemann, C. and G. Fry. 1995. Quantitative-analysis of terrain ruggedness in reindeer winter grounds. Arctic **48**: 172-176.

Pendergast J. F., S. J. Gange, M. A. Newton, M. J. Lindstrom, M. Palta, and M. R. Fisher. 1996. A survey of methods for analyzing clustered binary response data. International Statistics Review **64**:89-118.

Pharo E. J., and D. H. Vitt. 2000. Local variation in bryophyte and macro-lichen cover and diversity in montane forests of western Canada. Bryologist **103**:455-466.

Rettie W. J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology **76**:251-259.

Schaefer J. A., C. M. Bergman, and S. N. Luttich. 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology **15**:731-739.

Schaefer J. A., and W. O. Pruitt. 1991. Fire and woodland caribou in southeastern Manitoba. Wildlife Monographs:1-39.

Schneider, R. R. 2002. Alternative futures: Alberta's boreal forest at the crossroads. The Federation of Alberta Naturalists and The Alberta Centre for Boreal Research, Edmonton, Alberta, Canada.

Seip D. R. 1991. Predation and caribou populations. Rangifer, Special Issue **7**:46-52.

Seip D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology **70**:1494-1503.

Sibly R. M., H. M. R. Nott, and D. J. Fletcher. 1990. Splitting behavior into bouts. Animal Behaviour **39**:63-69.

Smith K. G., E. J. Ficht, D. Hobson, T. C. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear- cut logging in west-central Alberta. Canadian Journal of Zoology **78**:1433-1440.

Swets J. A. 1988. Measuring the accuracy of diagnostic systems. Science **240**:1285-1293.

Thomas D. C., E. J. Edmonds, and W. K. Brown. 1996. The diet of woodland caribou populations in west-central Alberta. Rangifer, Special Issue **9**:337-342.

Thomas, D. C. and D. R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada, in COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 1-98 pp.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics **20**:171-197.

Vistnes I., and C. Nellemann. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management **65**:915-925.

Warnock, N., J. Y. Takekawa, and M. A. Bishop. 2004. Migration and stopover strategies of individual Dunlin along the Pacific coast of North America. Canadian Journal of Zoology **82**:1687-1697.

Zielinski W. J., R. L. Truex, G. A. Schmidt, F. V. Schlexer, K. N. Schmidt, and R. H. Barrett. 2004. Resting habitat selection by fishers in California. Journal of Wildlife Management **68**:475-492.

Chapter 4. Synopsis

Understanding species habitat relationships is crucial to conservation efforts (Morrison 2001). Caribou are of major conservation concern in both Alberta (Dzus 2001; McLoughlin et al. 2003) and British Columbia (Seip 1998; Poole et al. 2000; Johnson et al. 2004b), due to declining numbers. Increased industrial development has been implicated in this decline (Smith et al. 2000; Dyer et al. 2001; Weclaw & Hudson 2004; Smith 2004), primarily through disruption of antipredator strategies (James et al. 2004) and increased encounter rates with predators (James 1999; James & Stuart-Smith 2000), facilitated by habitat alteration and fragmentation. With projected continuation in industrialization of the landscape (Schneider 2002), there is an urgent need to clearly define habitat relationships so that caribou conservation can be successfully integrated with industrial activities, or at a minimum, demonstrate the trade-offs inherent to various land management strategies (Schneider et al. 2003). Resource selection functions are ideally suited for this purpose, providing empirically based, quantitative and spatially explicit predictions of caribou occurrence on the landscape (Manly et al. 2002). Once validated, they become a powerful management tool that can be used in conservation planning, to inform land-use plans, including reserve design (Noss et al. 2002) and to minimize potential negative effects of development (Johnson et al. 2004b).

Selection of habitats, however, is relative to availability, and availability changes over space and time, necessitating continual monitoring of animals and updating of models in all but the most static of landscapes. This makes resource

selection functions an integral part of any adaptive management study design (Walters 1986) where habitat issues are paramount. Further, as Garshelis (2002) points out, while habitat selection studies are efficient at identifying habitats that are used often, they may fail to detect those that are used infrequently, regardless of their biological significance (for example, use of salt licks by ungulates). Therefore, it is important that these models be viewed as only one tool and used in conjunction with all available information, rather than considered magic bullets in identifying all habitat needs.

I investigated the habitat-selection patterns of woodland caribou in the Narraway range of west-central Alberta during two annual stages important for the conservation of the species: winter range use and spring migration. Most conservation efforts have targeted habitat use on caribou winter ranges, because they are thought to be the most limiting and are under increasing development pressure. Previous research on mountain caribou in Alberta has addressed winter range habitat selection based solely on stand attributes (Stepaniuk 1998; Szkorupa 2002) or in relation to anthropogenic disturbance independent of habitat features (Smith et al. 2000; Oberg 2001). By concurrently assessing habitat features and anthropogenic variables, I was able to generate coarse-scale models that reflect caribou response to more realistic, integrated landscapes, thereby improving on these previous studies. I also assessed fine-scale selection by caribou, focusing on potential forage species present at caribou use sites, providing insight into the ultimate mechanisms driving selection.

At a coarse-scale within their winter range, caribou selected for larger forest patches, with a higher area to perimeter ratio, and stands with a higher component of black spruce and a smaller component of fir. Less rugged terrain was also selected. While caribou avoided cut blocks, they were closer to seismic lines, and occurred in areas with a higher density of linear features within a 10 km^2 area, than expected. At a fine-scale, results were not definitive; however, caribou appeared to select for *Cladina mitis* and *Stereocaulon spp.* as potential forage items. Further, attributes not conducive to ground foraging: coarse woody debris, shrubs greater than 10 cm in height and bare ground, were avoided at this scale. The fine-scale evidence as a whole suggests that foraging opportunities may be the driving force behind selection at the coarse scale. At a coarse-scale, *C. mitis* occurrence was associated with regions that were closer to major water sources and in stands with a lower component of white spruce (*Picea glauca*). Incorporating the probability of *C. mitis* occurrence into my assessment of coarse scale caribou occurrence improved model accuracy. Correctly identifying the mechanisms driving selection and incorporating them into higher order models may be the key to producing models that generalize well across ranges (Garshelis 2000; Morrison 2001), particularly in species that inhabit diverse landscapes.

To my knowledge, I am the first to assess habitat selection during the spring migratory period. While the spring migration takes place over a relatively short period of time (1 – 14 days; Chapter 3), the shift in seasonal ranges is thought to be an important predator avoidance strategy (Edmonds 1988; Seip 1991). If connectivity is lost between calving and winter ranges, caribou may be

exposed to higher levels of predation than currently experienced. Although the fitness consequences of the alteration of migratory pathways or the completes loss of migratory behaviours are unknown, migration represents a fundamental characteristic of mountain caribou behaviour and maintaining connectivity between calving and wintering grounds should be a priority. I showed that caribou are highly selective during migration, using different habitats for traveling and resting/foraging. At the coarse-scale, caribou selected traveling habitat with low terrain ruggedness that was in closer proximity to permanent water sources. When resting/foraging, caribou selected for older stands containing a higher component of pine, and tended to be further from permanent water sources than random. These findings are consistent with migratory theory developed from observations of other species, with traveling locations found in areas that would minimize energy expenditure (Hedenstrom 2003) and resting/foraging locations consistent with coarse scale habitat attributes that are typically associated with higher forage abundance. I found arboreal lichen to be more abundant at resting/foraging sites when compared to traveling locations. My results suggest that, at a coarse-scale, caribou selected areas for resting/foraging that potentially support terrestrial lichens, and specifically select sites within these patches in which arboreal lichens are relatively abundant, with both terrestrial and arboreal lichens being potentially important food resources during migration. In order to maintain migratory conditions conducive to continued use, consideration must be given to both traveling and resting/foraging habitat.

1. Management Recommendations

One product of this research is spatially explicit habitat maps that identify where caribou are most likely to occur. Such maps can be used as a management tool, and incorporated into land use and conservation planning processes. They can be used to identify areas where industrial development could potentially occur with minimum effects on caribou, areas of high caribou use potential that should be protected, and areas of conservation concern where thoughtful management initiatives could ultimately enhance caribou habitat (e.g., through restoration).

If monitoring of the Narraway caribou population is continued, and models and digital landscapes updated, a time series of maps will provide an excellent opportunity to evaluate the effects of previous and current land use practices. Because of the limited development present on the Narraway range when this study took place, the baseline maps I have created provide a mechanism for measuring the cumulative effects of landscape change on caribou habitat use.

The Narraway winter range should be managed in a way that maintains large, older mixed conifer stands. My results lend support to the appropriateness of large-scale harvest blocks in caribou ranges, when implemented as part of an ecosystem-based management strategy that ensures adequate amounts of habitat are maintained over time. Because of the demonstrated avoidance of cut blocks, and the hypothesized community changes that would occur with conversion to early seral stage forests, forest harvesting in the large area identified as having a high likelihood of caribou occurrence on the northern portion of the Narraway caribou range should be avoided.

Perhaps most importantly, the transboundary nature of the Narraway caribou range requires the development of a coordinated management plan involving agencies from both Alberta and British Columbia. The absence of substantive development on the Narraway has meant that there has been little need for active management on this range. As a result, it has been largely ignored by management agencies. With interest in the area now growing, particularly from the energy sector, an active role by government is necessary for the proper management of this range. Communication and coordination is required between individual industrial operators, their regulating agencies and higher levels of government. This is necessary to ensure that conservation efforts on one side of the provincial boundary are not negated by developments on the other. Coordinated development initiatives would also reduce the overall industrial footprint on the landscape, reducing potential conflicts with caribou conservation. Integral to this coordinated management plan should be a yearly census of animals and recruitment surveys during the summer months. Currently, there are no accurate population estimates for the Narraway and recruitment surveys are not conducted. These will become critical pieces of information if the effects of habitat alteration and fragmentation at the individual and population level are to be evaluated and addressed.

2. Future Research

This research has provided a foundation for future research and highlighted many additional questions that should be answered so that the

successful integration of caribou conservation and industrial development can be achieved. Even though only a slight improvement in model fit was seen when fine-scale habitat attributes were incorporated into coarse scale models, some effort should be expended towards expanding fine-scale sampling, as fine-scale processes such as food choice are what ultimately drive habitat selection within home ranges. In association with caribou use sites, further exploration of the relationship with *Stereocaulon spp.* cover is necessary, as it has not previously been documented as important in determining caribou distribution, except in alpine areas (Johnson et al. 2004a). Increased sampling over the entire range of habitat types to accurately assess availability should be carried out. This would facilitate the development of digital forage species occurrence layers over the entire range, for incorporation into higher order models, potentially resulting in better predictive models that address the mechanisms of habitat selection.

I produced global models based on pooling data across individuals and years because of sample size limitations and the belief that this is appropriate for most management scenarios. However, variation in individual habitat selection can influence model parameters. When sample sizes permit, a quantitative assessment of this variation through modelling individual selection could improve model predictions and provide added insight into habitat requirements.

Habitat selection is evaluated relative to habitat availability. As habitat availability is not constant over space and time, it is hardly surprising that selection indices do not generalize well between ranges, and that performance varies over time. A quantitative assessment of the effect of habitat availability on

habitat selection is needed. How plastic are caribou in their response to certain environments and will the incorporation of mechanism-based parameters into landscape scale models improve model performance? These are questions with important management and land use planning implications, and thus should be addressed.

I investigated habitat selection during the spring migratory period, however, habitat use and route selection during the fall migration may be different than that identified for spring migratory events. A cursory inspection of limited data suggests that fall migration takes place over a wider time frame and is less directional than spring migratory events. Potential differences in spring and fall habitat requirements need to be addressed and incorporated into management and planning processes. Additional sampling of caribou use locations is also needed during the spring migratory period to more clearly define the relationship between forage species and caribou resting/foraging sites.

In addition to continued monitoring of caribou on the Narraway range to measure response to increasing industrial development, a unique opportunity exists to measure multiple species response to these changes. Although this would be a costly, long-term project, a study of this type could potentially answer many of the pressing questions regarding proximate and ultimate causes of caribou population decline.

Finally, while I present habitat selected by caribou at two scales, I have not linked habitat selected to critical population parameters, such as survival and recruitment. It is often assumed that habitat use is a surrogate for habitat quality,

but as many have pointed out (van Horne 1983; Delibes et al. 2001; Morrison 2001), occurrence may not always relate to fitness, particularly in human dominated landscapes (Bock & Jones 2004) where animals may miss ecological cues, resulting in ecological traps (Delibes et al. 2001). Future caribou research should focus on relating fitness to resource availability: a critical link to ensure population viability.

3. Literature Cited

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment **2**:403-410.

Delibes M., P. Gaona, and P. Ferreras. 2001. Effects of an attractive sink leading into maladaptive habitat selection. American Naturalist **158**:277-285.

Dyer S. J., J. P. O'neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management **65**:531-542.

Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, Alberta. 47pp.

Edmonds E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. Canadian Journal of Zoology **66**:817-826.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. *In*: Research techniques in animal ecology: consequences and controversies. L. Boitani and T. K. Fuller, *eds*. Columbia University Press, New York, NY. USA. Pp 111-164.

Hedenstrom A. 2003. Optimal migration strategies in animals that run: a range equation and its consequences. Animal Behaviour **66**:631-636.

James A. R. C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. PhD Dissertation. University of Alberta, Edmonton, Alberta.

James A. R. C., S. Boutin, D. M. Herbert, and A. B. Rippen. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management **68**:799-809.

James A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management **64**:154-159.

Johnson, C. J., K. L. Parker, D. C. Heard, and D. R. Seip. 2004a. Movements, foraging habits, and habitat use strategies of northern woodland caribou during winter: Implications for forest practices in British Columbia. BC Journal of Ecosystems and Management **5**:22-35.

Johnson C. J., D. R. Seip, and M. S. Boyce. 2004b. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology **41**:238-251.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.

McLoughlin P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management **67**:755-761.

Morrison M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management **65**:613-623.

Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology **16**:895-908.

Oberg P. R. 2001. Responses of mountain caribou to linear features in a west-central Alberta landscape. MSc Thesis. University of Alberta, Edmonton, Alberta, Canada.

Poole K. G., D. C. Heard, and G. Mowat. 2000 . Habitat Use by Woodland Caribou Near Takla Lake in Central British Columbia. Canadian Journal of Zoology **78**:1552-1561.

Schneider, R. R. 2002. Alternative futures: Alberta's boreal forest at the crossroads. The Federation of Alberta Naturalists and The Alberta Centre for Boreal Research, Edmonton, Alberta, Canada.

Schneider, R.R., J. B. Stelfox, S. Boutin, and S. Wasel. 2003. Managing the cumulative impacts of land use in the western Canadian sedimentary basin: a modeling approach. Conservation Ecology **7**:8 [online] URL: http://www.consecol.org/vol7/iss1/art8.

Seip D. R. 1991. Predation and caribou populations. Rangifer, Special Issue **7**:46-52.

Seip D. R. 1998. Ecosystem management and the conservation of caribou habitat in British Columbia. Rangifer, Special Issue **10**:203-211.

Smith K. G. 2004. Woodland caribou demography and persistence relative to landscape change in west-central Alberta. MSc Thesis. University of Alberta, Edmonton, Alberta, Canada.

Smith K. G., E. J. Ficht, D. Hobson, T. C. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear- cut logging in west-central Alberta. Canadian Journal of Zoology **78**:1433-1440.

Stepaniuk, D. W. 1998. Planning for woodland caribou winter habitat needs in west-central Alberta. MSc Thesis, University of Alberta, Edmonton, Alberta, Canada.

Szkorupa T. D. 2002. Multi-scale habitat selection by mountain caribou in west central Alberta. MSc Thesis. University of Alberta, Edmonton, Alberta, Canada.

Van Horne B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893-901.

Walters, C. 1986. Adaptive management of renewable resources. Macmillian Publishing Company. New York, New York, USA.

Weclaw P., and R. J. Hudson. 2004. Simulation of conservation and management of woodland caribou. Ecological Modelling **177**:75-94.